GYRFALCON BREEDING BIOLOGY IN ALASKA

By

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A

DISSERTATION

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DOCTOR OF PHILOSOPHY

By

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Abstract

This dissertation addresses specific research needs identified by a panel of experts on Gyrfalcon biology and conservation convened on 3 September, 2003 at the Raptor Research Foundation Scientific Conference in Anchorage, Alaska. The first chapter is a significant update and revision of the 1994 Gyrfalcon Birds of North America (BNA) species account, using all published papers and available grey literature from 1994 - 2007 and personal expertise from over 3,000 hours of coordinated observations. The second chapter reports results from a spatially explicit model, based on the best available compiled data from Alaska, that predicted Gyrfalcon breeding distribution and population size across Alaska. The model predicted that 75% and 7% of the state had a relative index of nest occurrence of <20% and >60%, respectively. Areas of high predicted occurrence primarily occurred in northern and western Alaska. Using environmental variables, the model estimated the size of the breeding Gyrfalcon population in Alaska is 546 ± 180 pairs. In Chapter 3, I used repeated aerial surveys to estimate detection probabilities of cliff-nesting raptors from fixed-wing aircrafts and helicopters. Detection probabilities ranged from 0.79 – 0.10 and varied by species, observer experience, and study area/aircraft type. Generally, Gyrfalcons had the highest detection probability, followed by Golden Eagles, Common Ravens, and Rough-legged Hawks, though the exact pattern varied by study area and survey platform. In the final chapter, I described for the first time in North America Gyrfalcon nest site fidelity, breeding dispersal, and natal dispersal using molted feathers as non-invasive genetic tags. Gyrfalcons were highly faithful to study areas (100% fidelity) and breeding territories (98% fidelity), but not to specific nest sites (22% fidelity). Breeding dispersal distance averaged 750 ± 870 m, and was similar between sexes. Natal dispersal of three nestlings representing 2.5% recruitment varied from 0 - 254 km. Mean territory tenure was 2.8 ± 1.4 yrs and displayed a bimodal distribution with peaks at 1 and 4 years. Mean annual turnover at one study site was 20%. Gyrfalcons in one study area exhibited low, but significant population differentiation from the other two study areas.

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All work conducted for this dissertation was permitted under the University of Alaska Fairbanks Institutional Animal Care and Use Committee protocol #08-04. T. Booms wrote chapters 2-4 in their entirety and incorporated suggestions by others. T. Booms significantly revised and re-wrote chapter 1, resulting in a doubling of the length and the addition of 14 years of literature to the document originally written by T. Cade and N. Clum.

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Introduction

The topics in this dissertation were identified as research needs on September 3, 2003 during a round table discussion on Gyrfalcon (*Falco rusticolus*) conservation, management, and research in Alaska during the Raptor Research Foundation Scientific Conference in Anchorage, Alaska. A panel of 18 leading experts on Gyrfalcon and raptor biology from across Alaska, Canada, and the lower 48 states addressed the status of Gyrfalcon conservation, identified data gaps that reduced our ability to conserve the species, and highlighted important research needs. A summary document was compiled that highlighted the primary research needs for the species. These needs directed the focus of this dissertation, and each chapter directly addresses a priority issue identified by the panel.

Three months prior to the conference, Brian McCaffery fortuitously introduced me to the significant raptor research potential that existed on the Yukon Delta National Wildlife Refuge (Yukon Delta NWR). After observing a study area supporting one the highest known nesting densities of Gyrfalcons on the planet, Brian and I identified a list of possible research topics that could be addressed in this unique area. Interestingly, these topics matched those identified by the expert panel that convened three months later. Brian and the Yukon Delta NWR subsequently offered financial research support, the summary document from the September meeting provided the needed and peer-reviewed research direction, and I was able to secure fellowships to cover academic expenses. Hence, the Yukon Delta NWR Gyrfalcon Project was born and from that came the research formally included here as my dissertation.

The four chapters are products of extensive pilot studies to identify feasible projects from the list of research needs generated in September 2003. After countless challenges, failures, discoveries, delays, snickers bars, mosquito bites, dead-ends, highs, lows, loss of funds, and obtaining new funds, my collaborators, graduate committee, and I settled on the four topics below for a dissertation. They are the direct products of the scientific process, with a healthy dose of logistical reality mixed-in for good measure.

They follow the unified theme of addressing specific calls by experts to address important scientific needs to further Gyrfalcon conservation in Alaska.

The first chapter, titled "The Gyrfalcon, Birds of North America Species Account" is a comprehensive review and synthesis of the literature that has been published pertaining to Gyrfalcon biology, ecology, and conservation. This chapter meets the need expressed by the panel by summarizing and updating all currently available published and unpublished information on the species. The chapter has been published by Cornell University as the revised and updated Birds of North America (BNA) Gyrfalcon account. Though I did not include formal findings from my field research on Gyrfalcons specifically in this chapter, it is only because of my extensive field work with the species during my dissertation research that I was able update and revise the account. This document succinctly summarizes the best available information on the species in North America from over 200 sources. Given the popularity and widespread use of the authoritative BNA series among scientists, managers, and general public, this chapter is likely to the be most used and cited work of the dissertation.

The second chapter, titled "Gyrfalcon Nest Distribution in Alaska based on a Predictive GIS Model" uses historical and contemporary nest locations, environmental layers, Geographic Information System (GIS), and TreeNet machine learning software to create a spatially explicit model predicting Gyrfalcon breeding distribution and population size across Alaska. This chapter addresses the need identified by the panel to assess the distribution of Gyrfalcons across the state, much of which has not been formally surveyed for Gyrfalcons. Because such an effort is probably financially and logistically unrealistic, we used historical information to model and predict the species current distribution. This chapter was published in 2009 online in *Polar Biology* and in paper form, in March 2010.

Chapter 3, titled "Detection Probability of Cliff-nesting Raptors during Helicopter and Fixed-wing Aircraft Surveys in Western Alaska," details efforts to conduct repeated aerial surveys (via helicopter and fixed-wing aircrafts) for breeding cliff-nesting raptors on the Yukon Delta NWR to estimate detection probability of Gyrfalcons, Golden Eagles

(*Aquila chrysaetos*), Rough-legged Hawks (*Buteo lagopus*), and Common Ravens (*Corvus corax*) in May 2007. This chapter addresses the need identified by the panel of evaluating survey methods that would include estimates of detection probability and allow for more robust and accurate monitoring of Gyrfalcon and other raptor populations. Most current cliff-nesting raptor surveys represent counts of birds at historical nest sites and are used as indices of population status. However, occupancy modeling and repeated surveys, as I did here, allow detection probabilities to be estimated. This, in turn, allows for direct population estimates and provides more robust and accurate results for population monitoring. Hence, we applied these techniques to breeding Gyrfalcons and other cliff-nesting raptors for the first time in North America and present our results in Chapter 3. This chapter has been accepted for publication in the *Journal of Raptor Research.*

The final chapter, titled, "Gyrfalcon Nest Site Fidelity, Breeding Dispersal, and Natal Dispersal on the Yukon Delta National Wildlife Refuge, Alaska," describes our work using non-invasive genetic sampling of adult molted Gyrfalcon feathers to study site fidelity and dispersal. This chapter addresses one of the most significant gaps in our understanding of the Gyrfalcon's breeding biology identified by the panel – nest site fidelity and dispersal. Prior to this work, our global understanding of Gyrfalcon nest site fidelity and dispersal was based on information from 6 banded individuals in Iceland and general assumptions based on anecdotal observations. Chapter 4 provides the first published information on these topics from known individuals for Gyrfalcons in North America and for any continental Gyrfalcon population and will be submitted for publication to *The Condor.*

Chapter 1. The Gyrfalcon, Birds of North America Species Account.[1]

INTRODUCTION

Largest of all falcons, and the most northern diurnal raptor, the Gyrfalcon inhabits circumpolar arctic and subarctic regions, with some individuals moving south into northern temperate zones during fall and winter. "Only then do most birdwatchers have a chance for a rare glimpse of this great falcon, which the Emperor Frederick II of Hohenstaufen, in his thirteenth century treatise on falconry (*De Arte Venandi cum Avibus*), extolled above all others as a hunter of cranes and similar large quarry. The Emperor wrote that the Gyrfalcon 'holds pride of place over even the Peregrine [*Falco peregrinus*] in strength, speed, courage, and indifference to stormy weather'" (Cade 1982).

Gyrfalcons exhibit pronounced reversed sexual size dimorphism (on average, adult males weigh 1,100-1,300 g, females 1,700-1,800 g), meaning males typically weigh about 65% as much as females. Gyrfalcon coloration is not conspicuously sexually dimorphic, because the species' coloration is extremely variable and ranges from nearly pure white to an almost uniform dark gray-brown. Intermediate ("gray") plumages are most commonly seen in North America. The Gyrfalcon is therefore considered a monotypic, but highly variable species (Am. Ornithol. Union 1998) and previous subspecies designations based primarily on plumage variation are no longer recognized. Most Gyrfalcons nest on cliffs above treeline, either in scrapes or in stick nests of other birds. Some individuals do not breed every year; both reproduction and winter

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[1] Booms, T.L., T.J. Cade, and N.J. Clum. 2008. Gyrfalcon (*Falco rusticolus*), The Birds of North America Online (A. Poole, Ed.). Ithaca: Cornell Lab of Ornithology; Birds of North America Online: http://bna.birds.cornell.edu/bna/species/114doi:10.2173/bna.114

movements are strongly influenced by food availability. Gyrfalcons respond functionally, and in some areas numerically, to changes in the availability of a variety of prey, but especially ptarmigan (*Lapogus* spp.), their principal food in most areas. The Gyrfalcon is a ptarmigan specialist and its breeding distribution is strikingly similar to that of the Rock Ptarmigan (*Lagopus muta*) (Holder and Montgomerie 1993). Gyrfalcon numbers appear to be cyclic in some regions but not in others, for reasons that are still not fully understood but likely related to ptarmigan population cycles (Cade et al. 1998, Nielsen 1999).

Although an uncommon species, the Gyrfalcon is not rare, as frequently stated. Remoteness of habitat, fluctuations in breeding populations and in migratory movements, variability in plumage and behavior, and rumors of rarity have all combined to make this species frequently misidentified or overlooked. Some of these same characteristics have enabled North America's Gyrfalcons to thus far escape the population declines that other raptors have suffered from persecution, chemical contamination, and habitat degradation. However, these traits do not protect the species from the potential effects of global warming, which is an emerging conservation concern because of the Gyrfalcon's northern breeding distribution, narrow ecological niche as a specialist predator, and reliance on Arctic habitats and prey.

DISTINGUISHING CHARACTERISTICS

Large falcon (length: males 48–61 cm, females 51–64 cm). No seasonal variation in plumage. Sexes best distinguished by size (see Measurements). Immatures exhibit vertical streaking and are more heavily marked on ventral surface than adults. Cere, eye ring, and feet of immature birds are light blue-gray. Adults' ventral surface is generally horizontally barred posteriorly and spotted anteriorly; bare parts yellow.

Dark eye and tomial tooth distinguish North American falcons from other raptors. White Gyrfalcon is unmistakable; no other falcon is white. Most dark Gyrfalcons distinguished from Peregrine Falcon by crown and/or nape heavily streaked with cream, and absence of pronounced facial stripe and cap. Birds with gray plumage are most easily

misidentified, but differ in plumage from Peregrines by having a two-tone underwing visible in flight and absence of a bold helmet. All Gyrfalcons distinguished from Prairie Falcon (*Falco mexicanus*) by absence of dark contrasting axillaries. Also distinguished from both Peregrine and Prairie falcons by larger size, proportionately longer tail and shorter, more broadly based wing with rounder tip. Primary formula usually $9 > 8 > 10 > 7$, compared to Peregrine Falcon ($9 > 10 > 8 > 7$) or Prairie Falcon ($9 \geq 8 > 10 \geq 7$). These characters give the Gyrfalcon an accipitrine appearance in flight, and when flying low it can be confused with the Goshawk (*Accipiter gentilis)*. Wing beat slower, deeper and more powerful than other falcons, but flight is faster and more sustained.

DISTRIBUTION

The Americas

Breeding Range.

Figure 1.1. From approximately 79°N to 60°N, locally to 55°N (Cade 1982, Brodeur et al. 1995); formerly south to 51° 28' N at entrance to Bras d'Or River (now Brador), Quebec (Audubon 1897, Todd 1963, Brodeur et al. 1995). In Canada, breeds on most Arctic Islands and the Arctic coastal plain (Fyfe and Grier 1972, Shank and Poole 1994), N. British Columbia, Yukon (Platt 1976, Mossop and Hayes 1994), se. Northwest Territories (Kuyt 1980), and n. Quebec and Labrador (Todd 1963). Summer sightings in Long Range Mountains of Newfoundland suggest breeding there (L. Tuck, pers. comm.). Most of Alaska except north coastline, w. Aleutians, Cook Inlet, central interior, and se. Alaska (Cade 1960, White and Cade 1971, Swem et al. 1994, Gibson and Byrd 2007).

Winter Range.

Winter status on breeding range poorly documented, but available information (Cade 1960, Platt 1976, Salter et al. 1980, Norment 1985) suggests most birds are resident, at least below 70°N. Regular winter visitor to British Columbia, Alberta, Saskatchewan, and Ontario (Bromley 1986, Wiseley and Pinel 1987). Most winter records are above 40°N (Am. Ornithol. Union 1983, Butcher et al. 1987) and are of immature birds. Extreme

southerly records from central and n. California (Small 1994), Texas (Lockwood et al. 2002), and North Carolina (Holmes and Fuller 1995).

Many published sources indicate Gyrfalcon does not winter regularly south of U.S.-Canada border (e.g., Root 1988, Schmutz et al. 1991), but much evidence suggests this is not the case with significant numbers of sightings in northern tier states (Platt 1976, Dobler 1989, Sanchez 1993, Flann 1998), establishment of fixed winter ranges (Dobler 1989, Sanchez 1993), and evidence that birds may repeatedly return to same wintering area (Palmer 1988, Sanchez 1993). Hence, the Gyrfalcon should be considered a regular, but uncommon winter visitor to the n. U.S.

Outside the Americas

Breeding Range.

Coastal Greenland to 82°N (Salomonsen 1950, Burnham and Mattox 1984), Iceland (Nielsen 1986), Norway, Sweden, Finland (relatively rare in n. Europe, Cramp and Simmons 1980), n. Russia, Siberia, and Kamchatka to below 55°N (Dementiev and Gladkov 1957, Ellis et al. 1992, Cade et al. 1998, Potapov and Sale 2005).

Wintering Range.

South irregularly into central Europe and Asia (Dementiev and Gladkov 1957, Glutz von Blotzheim et al. 1971, Potapov and Sale 2005).

Historical Changes

None documented in Nearctic breeding distribution, except for s. coast of Labrador and adjacent Quebec. Although significant increase in winter sightings (Christmas Bird Count records) from early 1970s to early 1980s may only be due to new awareness among birdwatchers that Gyrfalcon does winter in s. Canada and n. U.S. (Butcher et al. 1987), it

may also reflect this species' increasing occurrence around human-made reservoirs where waterfowl concentrate in winter (Sanchez 1993).

Fossil History

Three late Pleistocene (Rancholabrean North American Land Mammal Age, <400,000 Megannum) records for Gyrfalcon are earliest for species in North America. Two are records from cave deposits in Wyoming: Bell Cave, Albany Co. (Walker 1974) and Little Box Elder Cave, Converse Co. (Emslie 1985). Emslie suggests that several immature bones from Little Box Elder are evidence that Gyrfalcon may have nested in Wyoming during late Pleistocene. Mammalian faunas associated with bird fossils from Bell and Little Box Elder Caves reflect a colder climate. Third record is fossil species *Falco swarthi* (Miller 1927), which Emslie (1985) regarded as being essentially identical to Gyrfalcon. There are other Pleistocene records in Europe (Sweden, Czechoslovakia, Hungary; Brodkorb 1964, and the Iberian Peninsula; Baltar and Carrasquilla 1993). Dove et al. (2005) discovered ancient Gyrfalcon feathers in melting alpine ice patches in Southern Yukon. Though age of the feathers was not determined, other bird feathers found at the site were radio-carbon-dated as early as 4500 BP.

SYSTEMATICS

Geographic Variation

Little genetic differentiation among birds sampled in Alaska, Canada, and Norway suggests substantial gene flow among those populations. Gyrfalcons in Greenland and Iceland, however, appear genetically distinct (Johnson et al. 2007).

Complete gradation among plumage colors, though most birds are lumped into one of three color variants for convenience (white, gray, and dark). Relative frequency of each color variant differs among locations, and variants not present in all areas. Birds from n. Greenland and Canadian Arctic Islands mostly white; birds from central and s. Greenland semi-white (sometimes called "silver"), gray, or dark; birds from n. (mainland)

Northwest Territories roughly 50% white, 50% gray; birds from n. and nw. Alaska range from white (5-10%, P. Bente pers. comm.) to dark, but mainly gray; birds from other parts of range predominately gray. Darkest birds found primarily in Labrador, Quebec, and s. Greenland (Salomonsen 1950, Cade 1960, 1982, Bromley 1986, Poole and Bromley 1988b).

Regional prevalence of color variants (particularly white and intermediate plumages) possibly related to climate, as reflected by isotherms and temperature of oceanic currents rather than latitude; white types more common in colder areas (Salomonsen 1950, Ellis et al. 1992). Dark birds of Labrador and Quebec suggested as descendant of southern population isolated from more northerly refugium where white birds differentiated, while intermediate types persisted in separate southern refugia during Pleistocene (Palmer 1988, Ellis et al. 1992, Cade in Flann 2003). However, recent genetic analyses suggest Gyrfalcons may have expanded from only one refugium and that genetic differentiation was caused by genetic drift and philopatry (Johnson et al. 2007). Complete understanding of factors that caused and maintain geographic trends in plumage color is still lacking.

Outside North America, few white variants in n. Europe but increasing in proportion eastward to ne. Siberia and Kamchatka where approximately 50% are white (Dementiev and Gladkov 1957, Ellis at al. 1992, Gorovenko 2002). Breeding birds in Iceland gray with some light gray approaching white; occasional white birds in winter, presumably migrants from Greenland (Nielsen and Pétursson 1995).
For geographic variation in size, see Measurements.

Subspecies and Related Species

No subspecies currently recognized (Am Ornithol. Union 1957, Cramp and Simmons 1980). Previously described as polytypic (see references in Cade 1960 and Cramp and Simmons 1980, Potapov and Sale 2005) with up to 3 subspecies occurring in North America (*F. r. uralensis* in w. Alaska, *F. r. candicans* in n. Canadian Arctic Islands, *F. r. obsoletus* in remainder of range; Am. Ornithol. Union 1931, 1957). Review of

systematics (Vaurie 1961) concluded subspecific designations were inaccurate and meaningless.

MIGRATION

Nature of Migration in the Species

Birds breeding above 70°N in Greenland are migratory (Salomonsen 1950); degree of migration above 70°N in North America unknown. Below 70°N largely resident, but some partial migration (Cade 1960, Platt 1977, Kuyt 1980, Norment 1985), probably mostly of immature birds and some adult females. Birds remaining on territory during winter are almost exclusively adults and predominately males (Platt 1977, Poole and Bromley 1988b, Nielsen and Cade 1990b). Birds wintering outside breeding range are mostly immatures and subadults (Nielsen and Cade 1990b, Sanchez 1993). Winter sightings suggest possible female bias in migrating birds (Platt 1976, Sanchez 1993). Immatures may move farther than adults; Nielsen and Cade (1990b) found a greater proportion of juvenile birds in southern than in northern Iceland, and Sanchez (1993) found that subadults remained in fixed area whereas immatures wandered generally south through study area.

Timing and Routes of Migration

Movement out of breeding area begins late Aug and Sep (Salomonsen 1950, Salter et al. 1980, Nielsen and Cade 1990b, Schmutz et al. 1991, McIntyre et al. 1994, Britten et al. 1995). Earliest records on wintering grounds Sep, more typically Oct–Nov; last sightings Jan–Mar, rarely to May in s. Canada and n. U.S. (Salomonsen 1950, Platt 1976, Wisely and Pinel 1987, Palmer 1988, Nielsen and Cade 1990b, Sanchez 1993, Flann 1998). In Yukon, unpaired birds first observed on nesting territories in Jan, evidence of occupation in Dec (Platt 1976, 1977). In coastal Northwest Territories (NWT), unpaired birds first observed in Mar–Apr, evidence of occupation in Feb (Poole and Bromley 1988b). In

Greenland, breeding birds arrive in Apr (Salomonsen 1950). No known age-class bias in timing of movements.

In Greenland, migration primarily along seacoasts to s. Greenland and Iceland (Salomonsen 1950). Large numbers of migrating Gyrfalcons seen historically near Scoresbysund; many recently trapped there on migration (The Peregrine Fund 2005a). Recent satellite telemetry research by The Peregrine Fund should elucidate migration patterns in Greenland. In e. Canada, migratory movement along east coast of Labrador, Gulf of St. Lawrence, both coasts of Hudson Bay, and interior of Labrador Peninsula (Todd 1963). Movements in central and w. Canada known from small number of banded birds; movements typically, but not exclusively, southward (Poole and Bromley 1988b, Schmutz et al. 1991, Sanchez 1993). Of 5 recoveries of banded nestlings, 3 traveled south from nw. Canada, 1 traveled west from central Canada, and 1 traveled southeast from e. NWT to Ontario (Kuyt 1980, Schmutz et al. 1991). Five first-year birds banded in Canada moved 900–2,400 km during winter (Kuyt 1980, Schmutz et al. 1991). One nestling banded in NWT moved 145 km northeast but was probably recently independent (Poole and Bromley 1988b).

In Alaska, some movement of birds along Kenai Peninsula and Cold Bay. Four juvenile Gyrfalcons with satellite transmitters moved from Alaska into e. Russia within 4 weeks of fledging; three returned and wintered in Alaska (Britten et al. 1995). The remaining bird wintered near the Shantar Islands in the Sea of Okhotsk, having traveled more than 3,500 km. No directional trend in movements from the 9 transmittered juveniles though tended to use coastal and riparian areas (Britten et al. 1995). Some used the coastal areas of the Yukon and Kuskokwim Deltas in w. Alaska, as did at least 7 juveniles harnessed with transmitters and fledged from nests on the Yukon Delta National Wildlife Refuge (YDNWR). Two breeding adult females harnessed with transmitters on the YDNWR remained on or near their breeding site into the following winter (TLB, unpub. data).

At U.S. hawk watch locations, 2 records for Cape May, NJ (20 yr), and about 1 sighting/10 yr at Hawk Mountain, PA (S. Hoffman, P. Dunn, K. Bildstein pers. comm).

Two Gyrfalcons captured at Kittatinny Mountain Research Station in New Jersey, one in fall of 2000 and 1982, both immature females (McDonnell 2001). Of 13 Hawk Watch International Migration sites and partners from 1999 - 2005, two Gyrfalcons observed (1999 and 2006, Bridger Mountain) and one at former site at Rogers Pass, MT in 1998 (J. Smith pers. comm., Hawk Watch International 2007). Between 1993-2005, 45 Gyrfalcons observed during fall migration and from 1993-2007, 24 observed during spring migration at Mt. Lorette, Alberta (P. Sherrington, pers. comm).

Migratory Behavior

Diurnal migrant; nonflocking, though > 1 may be sighted during post-fledging period or where prey species are concentrated (Salomonsen 1950, Platt 1976, Cade 1982, Wiseley and Pinel 1987, Dobler 1989, Sanchez 1993).

Control and Physiology

Little information; extent of migration and destination believed to be determined primarily by food availability. Can persist as resident wherever flocking ptarmigan or waterfowl and seabirds occur. Limited satellite and radio transmitter results from Alaska suggest Gyrfalcon fall and winter movements may be influenced by shorebird, waterfowl, or sea bird concentrations in coastal areas. Montane and inland populations may be more likely to migrate (at least locally) than coastal and riparian populations because of greater temporal variation in food supply (Cade 1982, Nielsen and Cade 1990a). Weather influences many prey species and may indirectly affect Gyrfalcon movements. In South Dakota, first Gyrfalcon sightings corresponded with drop in temperature and increase in waterfowl abundance (Sanchez 1993). Wintering birds generally associated with concentrated prey populations (Salter et al. 1980, Dobler 1989, Everett et al. 1989, Sanchez 1993).

HABITAT

Breeding Range

Major habitat type is arctic and alpine tundra, often along rivers and seacoasts. Climate: polar continental, temperature -30°C to +10°C, annual precipitation 110–260 mm, snow covered 8–9 mo/yr, icebound 9–10 mo/yr. Vegetation: low arctic tundra; dominant species wide-ranging, including sedge (*Carex* spp.), birch (*Betula* spp.), willow (*Salix* spp.), cottongrass (*Eriophorum* spp.), lichens, and mosses (Cade 1960, Salter et al. 1980, Norment 1985, Poole and Bromley 1988b, Obst 1994). Occasionally in tundra-boreal forest ecotone; small discontinuous stands of spruce (*Picea* spp.) along drainages, beach strands, and dunes (MacFarlane 1891, Norment 1985, Obst 1994, Brodeur et al. 1995).

Rocky seacoasts, offshore islands, and barrenlands with rocky outcrops near coast, sea level to 500 m, including Greenland, Canadian Arctic Islands, Labrador Coast, Ungava Bay, Hudson Bay, and Bering Sea; particularly near colonial-nesting seabirds or waterfowl. Topography: sedimentary cliffs with volcanic intrusions and sills, basalts, rising above water and rolling or flat terrain (Cade 1960, Poole and Bromley 1988b). Rivers and some lakes draining through mountains and foothills in tundra or at edge of taiga, sea level to 1,050 m, including Koksoak and George Rivers in Ungava; Horton and Anderson Rivers in Northwest Territories; Firth River in Yukon; Colville, Utokuk, Kukpuk, and Sagavanirktok Rivers in Alaska; and Thelon River and lakes in Mackenzie district (Northwest Territories) (MacFarlane 1891, Cade 1960, White and Cade 1971, Roseneau 1972, Kuyt 1980, Obst 1994, Norment et al. 1999, Ritchie et al. 2003). Topography: river and lake bluffs of unconsolidated marine and nonmarine sediments; sand, silt, clay shale, and glacial till (White and Cade 1971, Norment 1985).

Mountainous terrain above timberline, up to 1,630 m, including Brooks and Alaska Ranges in Alaska (Cade 1960, Swem et al. 1994); British and Richardson Mtns. in Yukon (Platt 1976, Mossop and Hayes 1994); Richardson and Mackenzie Mtns. in Northwest Territories (Shank and Poole 1994); and Atlin region of British Columbia. Topography: escarpments and rocky crags of both sedimentary and volcanic origin (White and Cade 1971, Barichello 1983).

Spring and Fall Migration

Little information; migration and wintering habitat probably similar (see Salter et al. 1980, Johnson and Herter 1989, Sanchez 1993). Juvenile birds radio-tagged in Alaska used coastal and riparian habitats during fall, with multiple birds using the south coast of the Yukon-Kuskokwim Delta (Britten et al. 1995, TLB unpub. data). This area has wide expanses of tidal mud flats and coastal wetlands supporting large numbers of shorebirds, waterfowl, and gulls in the fall (Ernst 1989, B. McCaffery, pers. comm.).

Winter Range

Higher latitudes and elevations probably vacated (unless ptarmigan available, e.g., Denali Park, AK). Often frequent polynyas (open pockets of water) where seabirds congregate in otherwise frozen Bering Sea (Everett et al. 1989) and between Greenland and Canadian Arctic Islands (K. Burnham, unpub. satellite telemetry data). Winter range otherwise similar to breeding habitat for resident birds (Platt 1976, Cade 1982, Nielsen and Cade 1990b).

In north temperate region of the U.S. and Canada, open areas below 1,000 m, particularly in areas where prey (birds) are concentrated, including seacoasts, reservoirs, agricultural areas, grasslands, and shrublands. Topography generally flat or rolling. Substrate and vegetation vary widely with geographic region, including intermountain desert, prairie, river valleys, and human-modified habitats (Wiseley and Pinel 1987, Dobler 1989, Garber et al. 1993, Sanchez 1993).

FOOD HABITS

Feeding

Main Foods Taken.

Mostly birds and predominately ptarmigan, passerines to geese; some mammals, microtines to hares (*Lepus* spp.).

Microhabitat for Foraging.

Most prey taken on or near ground.

Food Capture and Consumption.

(From White and Weeden 1966, Platt 1977, Cade 1982, Jenkins 1982, White and Nelson 1991, Garber et al. 1993, Dekker and Lange 2001.) Three main methods of finding food: (1) perching at a spot with a commanding view; (2) quartering terrain at low altitude with flapping and gliding flight; (3) soaring along ridges or over valleys, not usually at high altitude, similar to Golden Eagles (*Aquila chrysaetos*). Four methods of pursuing prey: (1) on ground; if prey spotted at a distance, falcon flies close to ground using terrain to conceal approach and take prey by surprise; (2) tail-chasing (Fig. 1.2); failing to achieve surprise, falcon pursues prey over long distances, forcing it to ground or aloft to exhaust it; (3) hovering; if prey is in cover, falcon attempts to flush it into flight by making short stoops; (4) direct climb; to gain altitude on birds with light wing-loading and better soaring abilities, falcon flies up at steep angle, rather than "ringing" up, as does Peregrine Falcon.

Method of taking prey: either on ground or by short stoop; prey more likely to be struck or driven to ground than grabbed in air. Kills typically have broken sterna. Gyrfalcons, especially immatures, sometimes pirate food from other raptors. Little information on successful capture rate, but wintering birds observed successful in 10-28% of chases after feral pigeons (Dekker and Lange 2001, Dekker and Court 2003).

Manner of consumption: poor representation of cranium and distal wing elements at nest indicates that, during nestling season, prey are decapitated and distal portion of wings removed at kill site. Large amounts of plumage at kill site indicate that medium to large birds are plucked prior to transport to nest site (Langvatn 1977). Booms and Fuller (2003a) found 96% of ptarmigan delivered to video-monitored nests in Greenland were plucked, most of them completely so. Most ptarmigan delivered to nest included the breast and back, sometimes the legs and wings, and uncommonly the viscera. Feeding bouts on ptarmigan at the nest averaged 16 min (range 1-30 min). Ptarmigan brought to females during courtship relatively unprepared (Platt 1977).

Young (leveret) Arctic hares (*Lepus arcticus*) typically delivered without fur removed (86% of deliveries); if > 600 g, delivered in pieces (Booms and Fuller 2003a). Average feeding bout on a leveret at the nest 10 min (range 1-26 min). Adult arctic hare transported in sections (Poole and Boag 1988). Microtine rodents and passerines not decapitated or "plucked" (Langvatn 1977, Booms and Fuller 2003a). Sternum, forelimbs, primaries, secondaries, rectrices comprise > 80% of prey remains (i.e., uneaten portion) at nest site. Hind limb elements, vertebrae, mammalian and passerine bones predominate in pellets (i.e., portion consumed) (Langvatn 1977). Vegetable matter and grit in pellets indicate that some viscera of avian species are eaten (Langvatn 1977, Nielsen and Cade 1990b), but apparently viscera of ground squirrels (*Spermophilus* spp.) are not (Platt 1977, Poole and Boag 1988). Pellets at male perch sites during breeding season contain mainly beaks, claws, and gizzard linings, suggesting that these may be differentially consumed while other parts are fed to young (C. M. White pers. comm., TLB). Bones in pellets highly fractured and modified by digestion; few complete bones and those from the axial skeleton and especially the head are rare (Bochenski et al. 1998).

Delivery of prey fairly uniform throughout the day during the nesting season (Fletcher and Webby 1977, Bente 1981, Poole and Boag 1988), though Jenkins (1982) and Booms and Fuller (2003a) found delivery rates peaked in late morning and evening and declined sharply between 24:00 and 04:00 h. No information on timing of foraging during the nonbreeding season. Retrieval time of 6 prey deliveries observed from a nest

site averaged 15 min/prey item (Platt 1977). Length of hunting sorties observed from helicopter ranged between 22 and 67 min (n = 14); average time for female 27 min, male 38 min (White and Nelson 1991). Larger prey associated with longer foraging trips (Poole and Boag 1988). No cooperative hunting known.

Diet

Main Foods Taken.

Almost without exception, Gyrfalcons rely heavily on ptarmigan across their circumpolar range and throughout the year; numerous diet studies have repeatedly documented ptarmigan contribute the majority (50-95%) of total biomass eaten. Other birds taken range between 0.02 kg and 4 kg, including primarily waterfowl (*Anser* spp. and *Anas* spp.), seabirds, shorebirds (Scolopacidae), and passerines (Passeriformes). Other documented avian prey include sage grouse (*Centrocercus urophasianus*), gulls (*Larus* spp.), fulmars (*Fulmarus glacialis.*), terns (*Sternus* spp.), Black-legged Kittiwake (*Rissa tridactyla*), jaegers (*Stercorarius* spp.), alcids (Alcidae), Rough-legged Hawk (*Buteo lagopus*), falcons (*Falco* spp.), Ring-necked Pheasant (*Phasianus colchicus*), Short-eared Owl (*Asio flammeus*), ravens and crows (*Corvus* spp.), magpie (*Pica* sp.), Savannah Sparrow (*Passerculus sandwichensis*), Lapland Longspur (*Calcarius lapponicus*), Snow Bunting (*Plectrophenax nivalis*), redpoll (*Carduelis* spp.).

Gyrfalcons feed more on resident than migrant species. Mammals ranging from 0.01 kg to 4.5 kg, including primarily hares (*Lepus* spp.), ground squirrels (*Spermophilus* spp.), and lemmings (*Lemmus, Dicrostonyx*) but also documented are arctic fox young (*Aloplex lagopus*), shrews (*Sorex* spp.), and voles (*Microtus* spp., *Clethrionomys* spp.) (see references in Table 1.1; also Cramp and Simmons 1980 and Cade et al. 1998a for species taken in Palearctic).

Domesticated species taken rarely (81 attacks over 161 yr, Tømmeraas 1988), mostly chickens (*Gallus domesticus*) and Rock Doves (*Columba livia*) (Dekker and Lange 2001) but also domestic geese, ducks, rabbits, a turkey, and a cat; taken primarily by young birds in Palearctic region, where humans and falcons are in closer proximity.

Some eating of carrion (Kuyt 1980, Palmer 1988, Tømmeraas 1989), probably an adaptation to a harsh climate (Tømmeraas 1989). Will eat meat left by humans specifically for feeding Gyrfalcons (Randklev and Randklev 1994, Nielsen 2002).

Quantitative Diet Analysis.

See Table 1.1. Although Gyrfalcons take a wide variety of prey, individual birds or pairs exploit relatively few species. Willow (*Lagopus lagopus*) and Rock (*L. mutus*) ptarmigan are the dietary mainstay for most birds during the breeding season, but there are differences in diet relative to habitat (Nielsen and Cade 1990a, Huhtala et al. 1996). Coastal pairs take more waterfowl and seabirds and fewer ptarmigan, and pairs at higher latitudes and elevations take more mammals than do pairs in other habitat types.

Diets in Table 1.1 determined by prey remains and pellet analysis, which often present a biased view of diet (Marti 1987, Booms and Fuller 2003b). In central w. Greenland, prey remains and pellets overestimated ptarmigan and underestimated arctic hare occurrence at Gyrfalcon nests. Remains underestimated while pellets overestimated passerine occurrence in the diet (Booms and Fuller 2003b). Therefore, summaries in Table 1.1 should be reviewed with these potential biases in mind.

Diet shifts occur seasonally within a given habitat type. Adult ptarmigan taken most heavily early in breeding season, with proportion of alternative prey (shorebirds, waterfowl, passerines, and/or mammals) increasing later (Poole and Boag 1988, Nielsen and Cade 1990a, Booms and Fuller 2003b). Gyrfalcons nesting in upland habitat where migratory bird and resident rodent populations are low experience least seasonal variability, relying heavily on ptarmigan year-round (Nielsen and Cade 1990b). But even these birds may experience seasonal diet shifts; in Yukon, Gyrfalcons feed on Rock Ptarmigan during breeding season and on Willow Ptarmigan during winter (Platt 1976). Birds remaining on territory may experience diet shifts as a result of changing hunting habitat (Nielsen and Cade 1990a). Because habitat influences diet, birds that abandon territories during winter probably experience diet shifts; limited observations of foraging birds outside their breeding range indicate tendency to feed on species that congregate in

significant numbers such as waterfowl, game birds, and feral pigeons (Dobler 1989, Garber et al. 1993, Sanchez 1993, Dekker and Lange 2001, Dekker and Court 2003).

Annual variation in diet may occur where prey species exhibit large population fluctuations, but not in all locations. Some ptarmigan populations are known to exhibit cyclic changes in numbers (Mossop and Hayes 1994). Lemmings are heavily used in ne. Greenland in years when rodent numbers peak, and the diet shifts to passerines when rodent numbers are low (Gilg et al. 1997). When rodents are abundant, Gyrfalcons may feed heavily on rodent predators as well (Cade 1960). However, Gyrfalcons in Sweden did not shift diet when microtine rodents peaked in abundance (Nyström et al. 2006). Weather may also influence annual distribution, phenology, and availability of prey species such as ptarmigan and ground squirrels (Poole and Boag 1988, Nielsen and Cade 1990b).

Food Selection and Storage

Prey selection may be motivated more by vulnerability of prey than abundance. In Alaska and Iceland, Gyrfalcons take displaying male ptarmigan preferentially when non-flocking behavior, courtship displays, and molting plumage make them more vulnerable, even though they are not the most abundant prey species. At end of season, young ptarmigan of year are taken preferentially (Cade 1960, Nielsen and Cade 1990b). In Alaska, Iceland, Northwest Territories, and central w. Greenland, a switch from ptarmigan to other species coincides with decreased vulnerability (but not abundance) of ptarmigan, arrival of migrant species, and emergence of mammalian species (particularly juveniles) (Cade 1960, Poole and Boag 1988, Nielsen and Cade 1990b, Booms and Fuller 2003b). Both sexes take same size range of prey, but average size of prey brought by male is smaller, owing to greater proportion of passerines and small mammals (Platt 1977, Poole and Boag 1988). Immatures may preferentially take rodents and passerines (Bird and Bird 1941, Cade 1982). The relative proportion of Rock Ptarmigan (compared to Willow Ptarmigan) in Gyrfalcon diet in Sweden was positively correlated with the relative amount of Rock Ptarmigan habitat present in breeding territories (Nyström et al. 2006).

Rock Ptarmigan were also overrepresented in the diet and this was interpreted as a potential preference for Rock over Willow Ptarmigan.

Females perform 93–100% of caching during breeding season. Stored food usually placed behind vegetation within 100 m (maximum 200 m) of nest site (Poole and Boag 1988). Cached prey often retrieved and fed to chicks or consumed between regular feedings when chicks can feed themselves (Platt 1977, Jenkins 1978, Bente 1981, Poole and Boag 1988). Caching occurs between chicks hatching and reaching 43 d of age, being greatest when chicks are small, and thus prey is not completely consumed in a single feeding. No caching of microtines or passerines (Poole and Boag 1988). Removal of prey remains from nest variable; Platt (1977) documented no such behavior, Booms and Fuller (2003b) found 21% of food remains removed from nest. No information on caching by males, though 10% of cached items retrieved and delivered to the nest were by males (Booms and Fuller 2003b). Little information on caching outside breeding season; one observation of a cached frozen ptarmigan being retrieved and "chipped" apart during mid-winter in the Aleutian Is. (C. M. White pers. obs.), an immature female cached part of Mallard at the base of a routinely used perch tree on Skagrit Flats, and a female cached part of Ring-necked Pheasant at the base of a barbed wire fence post in California (B. Walton pers. comm.).

Nutrition and Energetics

Little information. Research by Barton and Houston (1993) on comparative digestive efficiency of raptors would suggest that an opportunistic species such as Gyrfalcon should have relatively high digestive efficiency on a wide range of species with variable nutritional quality. An estimated 1.0–1.5 kg of food/d (1.7–2.7 ptarmigan/d) are needed during the breeding season for a family of Gyrfalcons, for a total of about 75–110 kg—the equivalent of 150–200 ptarmigan—for the entire breeding season (courtship through fledging) (Cade 1960, Bengston 1971, Pulliainen 1975, Poole and Boag 1988). During the nestling period, Gyrfalcons delivered 99, 82, and 54 kg of food to three video-monitored nests, with 4, 3, and 2 young, respectively (Booms and Fuller 2003b, 2003c).

These represent estimates of 106, 94, and 110 kg of food delivered between hatch and fledging to each nest. Based on direct nest observations, Tømmeraas (1994, cited in Cade et al. 1998a) estimated a pair with 4 young eats 71 kg of food during the nestling period. Hence, theoretical calculated estimates above may be biased low, or birds studied by direct observation delivered more food than needed. Prey biomass per time spent foraging is higher for larger species, so small prey may only be profitable when they can be obtained quickly (< 10 min) (Poole and Boag 1988). Adult male Gyrfalcons commonly seen capturing fledgling passerines within 500 m of nests (TLB).

Metabolism and Temperature Regulation

No quantitative information, but see Breeding: young birds, growth and development; and parental care, brooding. Plumage generally softer and less compact than that of other falcons. Down highly developed and tarsus densely feathered on more than upper half, with some scattered feathers lower down (Cade 1982).

Drinking, Pellet-Casting, and Defecation

Drinking rarely observed in the wild, but captive birds drink; adequate water probably contained in food under most conditions. Pellets are long and oval, 2.2 cm x 5.0 cm on average; consist of feathers, fur, small to medium-sized bones, and occasionally vegetable remains from digestive tracts of ptarmigan (Langvatn 1977, Nielsen and Cade 1990b). Probably cast daily, but observations on captive birds indicate that frequency of casting is determined by amount of casting material consumed. No information on rates of defecation.

SOUNDS

Vocalizations

Development.

Call of young (see below, Vocal array: *Beg*) is a harsh, querulous screeching. Usually begins during hatching or immediately after, gradually becoming stronger and harsher with age. Given upon arrival of parent at nest, and during feeding. Occasionally given by older chicks while scanning, whether or not adults are present. Given by fledglings in presence of loafing parent. Softer, muffled version is given by young nestlings when distressed (The Peregrine Fund). Deep grunting calls like those of Common Raven (*Corvus corax*) heard from older nestlings and juveniles (Cramp and Simmons 1980). Young birds will also hiss when approached by intruders (see Behavior: Agonistic Behavior, communicative interactions). Young birds acquire *Kak* vocalization (see below) by 5–6 wk of age (Cade 1960). No information on timing of development of other vocalizations in wild birds.

Vocal Array.

Generally similar to other large *Falco* species. Calls of females lower in frequency (kHz) than males; difference can be used to differentiate between sexes in some breeding pairs (TLB). No information on geographic variation.

Kak. Repeated, relatively short (0.25 s), broad-band (1–7 kHz), harmonic call with moderate intercall interval (0.1 s); a guttural *Kak Kak Kak.* Similar to all *Falco* species (Cade 1982). In wild, given by both sexes as alarm or mobbing call and by male in Mutual Floating Display (Platt 1977) (see Behavior: sexual behavior, aerial displays). Limited to alarm call in captive birds.

Chup. Repeated (3–20 times), short (0.1 s), broad-band (0–6 kHz), harmonic calls with relatively long and variable intercall interval (0.2-0.5 s); a sharp, loud *Chup...Chup...Chup....* Differs from those of Peregrine and Prairie falcons in having single-syllable call (Wrege and Cade 1977). In wild, given by both sexes during Ledge Displays, by male during non-aerial Food Transfers (see Behavior: sexual behavior, pair

bond), and as a feeding call by both sexes. Calling is faster for both sexes in Mutual Ledge than in Individual Ledge displays. Calling of male becomes faster and louder as female approaches during Food Transfer (Platt 1977). In captivity, used by both sexes during Food Transfers, and as a contact call. Speed of calling by male during Ledge Displays does not change with presence of female. Speed of female calling increases at end of Mutual Ledge Display and Food Transfer, becoming a *Chatter* (Wrege and Cade 1977).

Chatter. Similar to Chup call in length, frequency, harmonic structure, and number of syllables, but intercall interval short (< 0.1 s); a sharp, stuttering *Chu-chu-chu-chu*. No comparable call in repertoire of Peregrine or Prairie falcons. Wild female *Chatters* when nestlings no longer accept food during a feeding event, often progressing directly from *Chup* calls (TLB). Female may also *Chatter* when refusing to relinquish incubation duties to male. In captivity given by both sexes, but predominately by female at conclusion of Mutual Ledge Displays and Food Transfers.

Chitter. Similar to Chup and Chatter calls in frequency, harmonic structure, and number of syllables, but shorter in duration (< 0.1 s); intercall interval so short to as be almost continuous; a sharp, slurred, *Chichichichi,* often occurring in bursts. Similar to Chitter call of Peregrine and Prairie falcons (Wrege and Cade 1977). In wild, given by female as male approaches to copulate, by male during copulation (Platt 1977), and by territorial male when encountering an intraspecific intruder (TLB). Also given when closely approached by human or dog and sometimes when bringing prey to the ground after capture (TJC). Context is similar for captive birds, but also sometimes given by either sex during Head-low Bow (Wrege and Cade 1977) (see Behavior: sexual behavior, displays at the nest ledge).

The *Chup*, *Chatter*, and *Chitter* best described as categories within a continuum of decreasing call duration and intercall interval, from the distinct *Chup* to the slurred *Chitter.* Though social contexts and functions of these calls differ, intermediate vocalizations given in transition between calls can be difficult to categorize in the field.

Wail. Continuous, relatively long (0.5–1.5 s), 2-syllable call with frequency and harmonic structure similar to other calls, but more energy in lower frequencies, a gradual increase in frequency over time, and longer and more irregular pauses between calls (0.2 s to 10 min, depending on context); a drawn out, rising *Waiiiik.* Similar to wail of Peregrine and Prairie Falcons (Wrege and Cade 1977). In wild, used occasionally by unpaired males following a Ledge Display, and continually during Eyrie-flyby and Wail-pluck displays (see Behavior: spacing, manner of establishing and maintaining territory). Used by paired males when approaching nest site with food (from distances up to 1.5 km). Also used in combination with *Kak* call during nest defense by both sexes and occasionally by adult females when on the nest or perch and apparently uncertain of the circumstance or whereabouts of its mate (TLB). A more strident version of this call is used by female during copulation (Platt 1977). In captivity, given by both sexes when motivated to change social context. As with wild birds, females use distinctive version of this call during copulation (Wrege and Cade 1977).

Whine. Similar to Wail in length, harmonic structure, frequency distribution, and intercall interval, but much lower amplitude; a soft, plaintive *waiiiik.* Similar to Whine in Peregrine and Prairie Falcons (Wrege and Cade 1977). In both wild and captivity, given by female during Copulation Solicitation (Platt 1977, Wrege and Cade 1977) (see Behavior: sexual behavior, copulation). In captivity, also given by either sex during Head-low Bow (Wrege and Cade 1977).

Beg. Repeated, relatively long (1.0 s), broad-band (1–9 kHz), harmonic call with moderately long (0.2 s) intercall interval. A high, harsh, protracted Screee...Screee...Screee. In wild, given by female when food-begging from male during Food Transfer (Platt 1977). In captivity, given only by nestlings (Wrege and Cade 1977).

Phenology.

Except for *Kak* call used during antagonistic interactions, vocalizations largely restricted to breeding season in wild and captive birds.

Daily Pattern of Vocalizing.

Little information. *Kak* call likely to occur whenever a threat arises, being timed to activities of other animals. Other vocalizations occur within context of displays; in captive birds, reproductive behavior generally more frequent early and late in day. Wild breeding Gyrfalcons are active at all hours because of long arctic summer days (Poole and Boag 1988) and thus show less temporal bias than captive birds; however, there is a quieter time from about 2400 to 0400 h (Booms and Fuller 2003a, TJC).

Places of Vocalizing.

Site of vocalization determined by site of behavior, but all occur within immediate vicinity of nest site. In wild birds, *Kak, Chitter,* and Wail call may be given from air, nest ledge, or perch. *Chup* call by male occurs at nest ledge or a perch, by female at nest ledge. *Chatter, Whine, and Beg* occur at either nest ledge or perch. For differences in sites of vocalizations in captive birds, refer to contextual differences described under Vocal Array, above.

Repertoire and Delivery of Calls.

All individuals appear to acquire same vocal array, though there is individual variation in context and frequency of certain vocalizations (Wrege and Cade 1977). In wild breeding birds, wide variation in use of *Kak* calls when disturbed by humans, some birds highly vocal while others almost silent. Females generally more vocal in nest defense than males (TLB). In captivity, 1-yr-old birds occasionally use vocalizations associated with reproduction, and 2-yr-old captive males use *Chup* call. Both sexes of 3-yr-old birds give *Chup* calls but not until well past normal breeding season. Full complement of behaviors and vocalizations obtained between 2 and 4 yr of age (Platt 1977, TJC). Seasonal changes in vocalizations reflect changes in rates of displays; in wild unpaired males, *Wail* is heard first, in paired birds *Chup* call (males before females, associated with Ledge Displays) is

heard next; female *Whine* (associated with solicitation), male *Chitter*, and female *Wail* (associated with copulation) occur later.

Social Context and Presumed Functions of Vocalizations.

See Vocal Array, above, for association between vocalizations and displays. *Kak* and *Chitter* considered aggressive calls; *Kak* used in territorial behavior and both calls used in nest defense, though *Chitter* less so. In captive birds, *Chitter* also seen in concert with threat displays (Wrege and Cade 1977) and used immediately after capture or when closely approached by humans (TJC). *Chup*, *Chatter*, *Whine*, and *Beg* probably function in appeasement, as they are associated with passive postures and nonthreatening behavior. Platt (1976), however, describes *chatter* as agonistic in wild birds. *Wail* of wild males appears to be advertisement, as it is associated primarily with unpaired males at nest sites and with paired males approaching from a distance with food. As in captivity, the *Wail* also appears to be given by either sex when social context changes or is uncertain in the wild.

Nonvocal Sounds

Hissing of air through wings during stoop quite audible at close proximity, as is turbulence created by wing beats when adults, particularly the female, approach or circle nest.

BEHAVIOR

Locomotion

Walking, Hopping, Climbing, etc.

More at ease on ground than most falcons. Walks on ground or nest ledge with body held horizontally (to prevent stiff tail from dragging) and slight side-to-side rocking (owing to relatively wide body). Relatively quick, agile runner, for a falcon. Will run on ground to

pursue prey or on nest ledge to displace another bird. Will hop onto rocks and other objects to perch, with aid of wings. Can climb some surfaces with aid of wings (most commonly seen in young birds), but more likely to hop or fly.

Flight.

See descriptions under Distinguishing Characteristics and Food Habits: feeding, food capture and consumption; and under Sexual Behavior. Generally more buoyant and less maneuverable than Peregrine Falcon, but faster in and more capable of sustained flight. Little quantification of flight. Quartering flight at 1–18 m above ground, soaring at 60–900 m (White and Weeden 1966, Platt 1977, Jenkins 1982, White and Nelson 1991). A soaring male flew a minimum of 44 km in about 67 min, giving a minimum speed of 40 km/h (White and Nelson 1991). Trained falcons flying 500 m to a lure demonstrated average minimum power speeds of 11.4 m/s, relative air speed of 1.53, and wing beat frequencies of 5.27 HZ (Pennycuick et al. 1994). This latter study suggests that in "chase mode" additional power is gained by reducing wingspan (sacrificing the efficiency associated with constant circulation of air around the wing) and increasing wing beat frequency. Temporary disregard for fuel efficiency combined with a substantial aerobic scope enable the slower-flying Gyrfalcon to chase down its faster-flying prey. When stooping, a captive male Gyrfalcon reached a maximum speed of 209 km/h (Tucker et al. 1998). The bird's stoop consisted of three phases: 1) acceleration phase during which the bird dove at 17-62° from horizontal accelerating with minimum drag, 2) brief constant-speed phase when the bird increased drag to maintain speed, and 3) deceleration phase when the bird increased drag dramatically by cupping its wings in a high angle of attack before grabbing a swinging lure. Theoretically, Gyrfalcons in the wild could reach speeds of 250 km/h or more on very long stoops (Tucker et al. 1998).

Self-Maintenance

Preening, Head-Scratching, Stretching, Bathing, Anting, etc.

Not reported in detail. Preens frequently, using uropygial gland. Generally rouses (shakes) after preening, and will rouse during flight. Middle toe used to scratch (directly), mostly around cere and head. Stretches by laterally extending wing and leg on same side, and by bowing body forward and extending both wings up and forward with upper surfaces facing each other. Bathing consists of rocking body back and forth, dipping head in water, and fluttering wings and tail while holding feathers erect and away from body. Bathing in wild birds does not appear to differ from behavior of captive birds. One bathing bout observed in Greenland lasted 17 min (Jenkins 1982). Birds bathe in pools of runoff water on still-frozen rivers, in pools on tundra, and at edges of flowing rivers (Platt 1977, TJC). Platt (1977) twice observed a male dustbathe, using same site at same time of day. Dustbathing occurred on sunny days with temperatures near 5°C on a south-facing slope. Both sexes observed dustbathing repeatedly over the course of a breeding season in a small gravel opening on a south-facing slope (TLB). Birds scooted down the 3-m gravel slide while exhibiting bathing motions described above. Captive birds have also been observed to bathe in snow (B. Walton pers. comm.).

Sleeping, Roosting, Sunbathing.

Sunbathing not documented in wild but has been observed in captivity. Sleeps with head tucked in back or scapular feathers, in normal perching position with head facing forward but hunkered slightly, or lying down in incubating position, sometimes with head on scrape. Sleeping with head under scapulars tends to occur mostly at "night" and is associated with longest sleep periods. During brooding, female sleeps 28% of time, or over 6h/d (Jenkins 1982). Little information on roosting. During breeding season, probably roosts near nest site; female does not spend "night" on nest ledge after brooding ceases. Male does not roost at nest ledge. Young roost together after fledging (Fletcher and Webby 1977). Presence of fresh mutes, prey remains, pellets, tracks in snow, plus

occasional sightings and molted down and feathers, indicate that most nest sites are used for roosting during winter (Cade 1960, Platt 1977, Nielsen 1986, Poole and Bromley 1988b). In nonbreeding areas, wild birds will roost on ground (G. H. Sanchez pers. comm.) as will trained birds left out at night (TJC). Trained birds also observed roosting in Raven's nest (B. Walton pers. comm.).

Daily Time Budget.

Not well quantified. Shortly before egg-laying, female spends most of time sleeping on nest ledge (Platt 1977). For time spent incubating and brooding, see Breeding: incubation, and parental care. By 2–4 wk posthatching, both parents are largely absent from nest site except to deliver food (Fletcher and Webby 1977, Jenkins 1978). Seasonal differences in time budget expected owing to extreme differences in day length between breeding and wintering seasons.

Agonisitic Behavior

Physical Interactions.

Both sexes will chase and strike at intra- and interspecific intruders during breeding (Cade 1960, Platt 1977, Nielsen and Cade 1990b) and nonbreeding seasons (Sanchez 1993). Gyrfalcons are believed to have killed intruding Common Ravens, Rough-legged Hawks (*Buteo lagopus*), and Peregrine Falcons (see Cade 1960). Gyrfalcon will also flee, at least from Peregrine Falcon, if former is intruder (Cade 1960). In aerial combat Gyrfalcon sometimes locks talons with intruder; the birds cartwheel down through air and may strike the ground bound together (TJC).

Communicative Interactions – Threat Displays.

Involve a combination of behaviors, depending on intensity: facing toward source of threat, gaping, erecting feathers, head held along body axis, and hissing. Least intense

form is Upright Threat. In its mildest form, bird pulls itself upright with beak toward threat, wings closed, feathers sleeked except for flared cheek feathers, and gapes briefly. In captivity, often used when a bird lands on a perch near its mate. More exaggerated form of Upright Threat, typically seen in young birds, is for bird to pull itself upright with beak toward threat, spreading wings to sides and flaring all feathers, including tail, gape (protracted), hiss, and if pressed, fall backward, to defend itself with feet. Most intense form is Horizontal Threat, in which bird orients its body horizontally, flares feathers of back, crown, and cheeks, and points its beak toward threat. Unlike Upright Threat, which is largely defensive, Horizontal Threat places bird in a position ready for attack. Threat displays observed in both wild and captive birds, but are relatively infrequent compared to Peregrine Falcon.

Appeasement Displays.

Appeasement or submissive displays involve behaviors that are generally direct opposites of threat displays: turning beak away, sleeking feathers, holding head below body axis (often pointed down), silent or giving soft, chick-like call. Most typically seen during breeding; see below, Sexual Behavior: pair bond (NJC, TJC).

Spacing

Nature and Extent of Territory.

Territories centered on nest cliffs, usually regularly spaced (Poole and Bromley 1988b). Mean internest distances range between 5 and 96.7 km; distances related to nest-site availability and habitat productivity and vary geographically and annually (Cade 1960, Burnham and Mattox 1984, Nielsen 1986, Mossop and Hayes 1994, Shank and Poole 1994). Actual area most often defended is a horizontal oval < 1,400 m long (centered on nest ledge) and 400–500 m deep (Platt 1977).

Manner of Establishing and Maintaining Territory.

Little information on establishment of territories. In Yukon, an unpaired male occupying a nest site early in breeding season daily gave 4 different advertisement displays (Platt 1977). Eyrie-flyby Display consists of male flying (horizontally) parallel to cliff face in a figure eight about 10 m from eyrie, with crossing point in front of eyrie. Repeated 2–3 times, accompanied by Wail; prey often carried. Wail-pluck Display occurs when male returns with prey, or occasionally when discarded prey is recovered from perch. Male begins to Wail and slowly plucks prey, pausing to look around but continuing to Wail. In this way, male takes twice the normal time to pluck and eat a ptarmigan. Two other displays, Male Ledge and Undulating Roll, also performed by paired males (see Sexual Behavior: pair bond). Wail vocalization more prevalent in unpaired males.

Territories maintained by aggressive vocalization (*Kak*) and pursuit of intruders. Few documented intraspecific interactions (1 each: Jenkins 1978, Platt 1977, 1989, Woodin 1980). Higher frequency of intraspecific interactions ($n = 10$) in Iceland may be related to higher density (mean internest distance 6.2–8.1 km, Nielsen 1986). Likewise, in w. Alaska with internest distances similar to Iceland, 4 intraspecific interactions near nests observed in one year, all were resident pairs pursuing intruding sub-adults (TLB). Resident females respond similarly to all intruders; resident males show relatively little aggression toward intruding females, but repeatedly attack and chase (up to 1 km) intruding males (Nielsen and Cade 1990b).

Interspecific Territoriality.

Interspecific interactions involve other predatory birds, i.e., Common Raven, Rough-legged Hawk, Golden Eagle, Red-tailed Hawk (*Buteo jamaicensis*), Northern Harrier (*Circus cyaneus*), Snowy Owl (*Nyctea scandiaca*) (Evans 2000), and Peregrine Falcon. Attacks documented on a red fox (*Vulpes vulpes*) and a wolverine (*Gulo gulo*) near nest cliff, although a passing timber wolf (*Canis lupus*), porcupine (*Erethizon dorsatum*), grizzly bear (*Ursus arctos*), and caribou (*Rangifer tarandus*) elicited no response (Platt 1977). Vocalization (*Kak*) and behavior (pursuit/attack) similar to that directed at

conspecifics. Level of aggression influenced by proximity, behavior of intruder, and individuality of falcons. Some pairs will not tolerate presence of predatory birds, attacking them whenever opportunities arise, especially Golden Eagles, whereas others will tolerate nesting on same cliff if intruders do not fly toward nest (Cade 1960, Platt 1977, Poole and Bromley 1988a, Nielsen and Cade 1990b).

Winter Territoriality.

No information on territoriality of birds wintering at nest sites. Birds wintering outside breeding area aggressively pursue conspecifics and other predatory birds (Dobler 1989, Sanchez 1993). Behavior toward other species is similar to that seen during breeding season. Roughly half of interspecific interactions observed in South Dakota involved food defense. Behavior toward conspecifics differs from that during breeding season; instead of "resident" driving "intruder" away, the 2 birds alternate pursuit of each other, suggesting this behavior represents defense of individual space rather than territory defense (Sanchez 1993).

Dominance Hierarchies.

Not known to occur, but females believed dominant over males (Cade 1982), and adults may displace immatures (Sanchez 1993).

Individual Distance.

Pairs and nest-mates will sit side by side. Once brooding ceases, adults generally perch within 100 m of nest ledge, except when delivering food (Platt 1977). Independent birds defend individual space (see Demography and Populations: range) throughout annual cycle (Sanchez 1993).

Sexual Behavior

Mating System and Sex Ratio.

Monogamous. No information on primary sex ratio. Sex ratio of nestlings 1:1 (Poole and Bromley 1988b, Cade et al. 1998b).

Displays at the Nest Ledge.

Descriptions of wild birds from Platt (1977) unless otherwise noted. Descriptions of captive birds from Platt (1977) and Wrege and Cade (1977). Descriptions presented in order of occurrence. For descriptions of vocalizations and contextual differences between wild and captive birds, see Vocalizations.

A Visit to the nest consists of falcon standing alone in normal perching posture, or walking into eyrie and standing upright. Performed by either sex, lasting 1–21 min; not described in captive birds as separate display. No vocalization accompanies this activity. *Vertical Head-low Bow* given with body in normal perching position, feathers sleeked, and head depressed and oriented away from mate; given by either sex. *Horizontal Head-low Bow* is more intense form, given with body held horizontally, feathers sleeked, and head bent at almost 90° to body and oriented away from mate; given by either sex. In captivity, head may be bobbed or held stationary; vigorous bowing of Peregrine Falcon not seen. Head-low Bows occur as isolated displays in captive birds, but are not described outside context of Ledge Displays and Food Transfers in wild birds. In captivity, both Vertical and Horizontal Head-low Bows are much more discrete, less intense, and used less frequently than in Peregrine Falcon. Males use these displays more frequently than females in both species. *Scraping* is done by either sex and consists of bird leaning forward, rocking from side to side, placing its weight on its breast with tail relaxed, and pushing vigorously backward with feet to form a small depression. After Scraping several times, bird may turn to face a different direction and continue Scraping. No vocalization accompanies this activity. Occurs as solitary activity or as part of Individual Ledge Display. *Male Ledge Displays* consist of male approaching scrape in Horizontal Head-

low Bow position with high steps (causing body to rock back and forth), giving Chup vocalization. Male pauses to look at female, whose reaction determines intensity and duration of display. *Female Ledge Displays* similar to those of male, but female does not tend to pause to look at male, displays are less intense, less frequent, and occur later in season. Mutual Ledge Displays occur when female approaches scrape during Male Ledge Display. Unlike Peregrine Falcons, Gyrfalcons remain stationary during display and rarely pause. Male generally terminates display by leaving scrape while female remains. *Billing* consists of female turning head sideways, orienting beak up while male's is directed downward; birds nibble between beaks. In captive birds, Billing occurs during Mutual Ledge Displays and when birds are perched closely together. Vocalizations tend to degrade during Billing. Not observed in wild birds. Scraping, Male Ledge Displays, Female Ledge Displays, and Mutual Ledge Displays are essentially identical between captive and wild birds (but see Vocalizations for differences in accompanying vocalizations).

Aerial Displays.

Five aerial displays described in wild birds, occurring mostly within egg-laying period. *Roll* is executed by male while in long dives, at angles between 30 and 60°. A partial roll of 20° precedes a roll of 180° in opposite direction. Male remains with dorsal surface down for 1–2 s, then roll is reversed and dive continues in normal flight position. In *Undulating Roll*, male begins a brief glide with extended wings from level flight at moderate speed; body then briefly rotates laterally about 20°, then rotates 180° in opposite direction. When second rotation is half completed, male begins a steep dive, becoming vertical with ventral surface facing in original direction of flight. This position is held as male dives 30–50 m, then he returns to normal flight position by rotating in opposite direction from 180° roll. At this point, dive is terminated and bird is carried upward at steep angle. When original elevation is reached, maneuver is repeated. This display may be modified by eliminating 20° roll at beginning of second dive, or by pitching over backward into an inside loop. Males also *Flash* by rolling laterally 90° to

one side and then the other during flight, producing a flashing or flickering effect as dark back and light breast are alternately exposed (TJC). In *Mutual Floating Display*, male positions himself 2–3 m above soaring female, and both birds drop slowly at about 20° angle. Both birds hold wings partially closed and slightly above back with legs extended and tails spread. Display lasts 10–13 s, male gives Kak vocalization; constant distance between pair is maintained. In *Passing and Leading Display*, male overtakes flying female, passing close by, and begins weaving back and forth in front of her. Aerial displays do not occur in captive birds.

Food Transfers.

Food Transfers begin about 10 d prior to egg-laying and continue through nestling period. In wild birds, all transfers are from male to female and always involved a freshly killed prey item. About 85% of Food Transfers in wild birds occur on perches. Male approaches nest site with prey in feet, giving Wail vocalization. As he perches, he changes to Chup vocalization. Female then crouches with body feathers puffed out and wings partially extended. Female flies to male in a Flutter-glide (also called Sandpiper Flight, Cade 1960), with shallow wing beats, tail slightly fanned and pointing downward, with a Beg call. Male picks up food in beak and presents it in Vertical Head-low Bow posture, female lands next to male approaching in a slightly aggressive horizontal posture and takes food in foot or beak in a Horizontal Head-low Bow posture. In captivity, female-male transfers occur, though less frequently than male-female transfers. Captive birds also use cached items or scraps in transfers. Captive females do not beg from males. In both captive and wild birds, female typically goes to male if transferring outside of nest, otherwise wild male may deliver directly to brooding female (TLB). Aerial Food Transfers occur prior to egg-laying and after brooding, when female is able to detect approaching male before he lands. As female watches male approach, she makes flight intention movements, then flies towards him in a Flutter-glide, reaching him as far as 400 m from cliff. Female flies about 10 m above male, climbs slightly, dives in front, and

pitches up underneath him, turning upside down to grab prey. Male appears to adjust speed, sometimes almost hovering. No aerial transfers in captive birds.

Copulation; Pre- and Postcopulatory Displays.

Either sex can solicit copulation; display by either sex generally induces other sex to display. Males use *Curved Neck Display*: standing erect while arching neck and pointing beak down and away from female so that back of neck is highest part of bird; no vocalization given. In captivity, this display accompanied by a Chitter, and when female is very close, male may assume Vertical Head-low Bow position or turn perpendicular to her. Females generally respond to Curved Neck Display with *Copulation Solicitation*, in which female assumes a horizontal position with head below plane of body, beak pointing down, and tail raised slightly above back; a soft Whine is given. In captivity, females appear to be more aggressive in this posture, often approaching male head-on (see above, Agonistic Behavior: communicative interactions, threat displays). As male approaches for copulation, female's Whine changes to Chitter and her body tilts forward to about 45°. Male hovers briefly about 50 cm above female, orients to face same direction as female, and lands on her back in a vertical Curved Neck position, supported on his tarsi between female's humeri and thorax, with toes contracted and feet turned inward. Male's wings constantly flap and tail points straight down and shuffles from side to side. Male gives Chitter vocalization. Female's wings are slightly opened and tail is vertical and slightly to side. Female's Whine becomes a copulatory Wail. In wild, copulation can occur up to 29 d prior to egg-laying and continues through egg-laying; each copulation lasts 4–12 s, during which male makes 4–5 thrusts. In captivity, young males attempt to climb rather than fly onto female's back (Wrege and Cade 1977). Observations on captive birds at high latitude also indicate that copulations are more frequent during warm weather and immediately before egg-laying (Seifert 1982).

Duration and Maintenance of Pair Bond.

Within a breeding season, all pairs remain together at least until young have dispersed. Roughly half of territories occupied during nonbreeding season had pairs (Platt 1977, Nielsen and Cade 1990b), which had presumably remained together year-round. No information on longevity of pair bond; presumably birds remain mated until one dies, then readily re-pair.

Extra-Pair Copulations.

Not known to occur. A female-female pairing of a Gyrfalcon and Peregrine Falcon that laid eggs in and shared incubation duties on a nest was documented in 1989 and 1990 in Norway (Gjershaug et al. 1998); no eggs hatched.

Social and Interspecific Behavior

Degree of Sociality.

Solitary or in pairs during breeding and nonbreeding season (Platt 1977, Nielsen and Cade 1990b). Fledglings may roost together (Fletcher and Webby 1977). Small groups (6–8) of immatures sometimes seen in fall (Cade 1982).

Play.

Similar to Peregrine Falcon. Immature birds will attack inanimate objects and make abortive attacks on live animals with no apparent attempt to kill (Cade 1953). Unlike Peregrine Falcons, trained adult Gyrfalcons remain playful (TJC).

Interactions with Members of Other Species.

Mobbed by small diurnal passerines. Wintering Gyrfalcons were robbed of prey by Bald Eagle (*Haliaeetus leucocephalus*) (Dekker and Court 2003); 1 record of attempted

robbery by conspecific (Jenkins 1978). Commensal nesting in North America: Canada Goose (*Branta canadensis*) within 2.5 and 4.5 m, Common Eider (*Somateria mollissima*) and White-fronted Goose (*Anser albifrons*) within 36 m, Green-winged Teal (*Anas carolinensis*) within 180 m, all unmolested (White and Springer 1965, K. Poole pers. comm.).

Predation

Two yearling falcons (males) found as food remains in 2 different Common Raven nests, probably picked up as carrion (Nielsen and Cade 1990b). Remains of juvenile Gyrfalcon found in two pellets removed from a Gyrfalcon nest (Booms and Fuller 2003a). Golden Eagle is potential, but not documented, predator of wild Gyrfalcons, as demonstrated by degree of aggression and caution accorded them (Platt 1977). Trained Gyrfalcons often killed by Golden Eagles on quarry or in flight (TJC). C. M. White (pers. comm.) saw a flying adult Gyrfalcon struck by a female Peregrine in the Aleutians, breaking the Gyrfalcon's wing. The Gyrfalcon was subsequently caught and killed by a Bald Eagle.

BREEDING

Phenology

Pair Formation.

Figure 1.2. Evidence for year-round occupation of nest sites in Alaska (Cade 1960), Yukon (Platt 1976), and inland Northwest Territories (NWT) (Kuyt 1980, Norment 1985). On coastal mainland of NWT, however, no evidence of occupation prior to Feb (Poole and Bromley 1988b), perhaps because more severe weather conditions at coastal eyries or higher latitudes restrict hunting opportunities at winter solstice (Poole and Bromley 1988b, Nielsen and Cade 1990b). Sites occupied prior to breeding are generally same sites that are subsequently active during breeding season (Platt 1976, Poole and Bromley 1988b, Nielsen and Cade 1990b). In Yukon, first observations of paired birds in

Feb (Platt 1976), about 1 mo after first observations of unpaired birds and 2 mo prior to egg-laying. In coastal NWT, first observations of paired birds in late Apr, about 2 wk prior to egg-laying (Poole and Bromley 1988b), but birds probably paired earlier (K. Poole pers. comm.). Courtship activities begin about 1 mo before egg-laying (Platt 1977).

Nest-Building.

No nest-building per se. Scraping (pushing substrate aside with feet to make a shallow depression) begins early in courtship and continues until egg-laying.

First/Only Brood per Season.

Figure 1.2. Egg dates (ranges include possible renesting attempts): Yukon, 3–28 Apr (Platt 1977); coastal NWT, 21 Apr–30 May (Poole and Bromley 1988b); inland NWT, 20 Apr–2 Jun (estimated), Kuyt 1980, Norment 1985); Alaska, Apr to late May (estimated; Cade 1960). There is general trend for nesting to occur later at higher latitudes (Bromley 1986), although there is much overlap in egg dates among regions. Egg dates vary significantly from year to year (Poole and Bromley 1988b, Nielsen and Cade 1990b). Degree of synchrony within population also varies annually (Poole and Bromley 1988b). Chicks hatch after 34–36 d (Platt 1977). Males fledge at 45–47 d, females at 47–50 d (Poole and Bromley 1988b). Young independent $\geq$ 4 wk after fledging (Cramp and Simmons 1980, Nielsen and Cade 1990b, Britten et al. 1995).

Four records of renesting: 1 in Alaska Range (Cade 1960), 1 in NWT (Poole 1988a), and 2 in Yukon (Platt 1977). Renests occurred after failure (abandonment) of previous clutch (Platt 1977, Poole 1988a). Recycle time approximately 16 d for both wild (n = 1, Poole 1988a) and captive (n = 11 for 2 pairs, The Peregrine Fund) birds. Phenology similar to first brood, but post-fledging period may be shorter (Poole 1988a).

Second Brood per Season.

None; renesting only.

Nest Site

Selection Process.

Unclear which sex chooses nest site, as unpaired birds of both sexes have been observed frequenting nest cliffs prior to breeding season (Platt 1977, Nielsen and Cade 1990b). Males seem to predominate (Platt 1977, Poole and Bromley 1988b), however, and have been observed to advertise for females (Platt 1977).

Microhabitat, Nest-Site Characteristics.

Most (58–91%) nesting occurs in nests of other species, particularly Common Raven, Golden Eagle, and possibly Rough-legged Hawk; remainder of nest sites on ledges (Cade 1960, White and Cade 1971, Barichello 1983, Poole and Bromley 1988b, Nielsen and Cade 1990b). Will usurp newly built nest of ravens but not of eagles (Poole and Bromley 1988b, Nielsen and Cade 1990b). Most (> 80%) nest sites on precipitous cliff faces (Cade 1960). Mean nest height 4–30 m (Cade 1960, White and Cade 1971, Poole and Bromley 1988b). Most (85–94%) sites with overhangs (Cade 1960, Poole and Bromley 1988b, Nielsen and Cade 1990b, Obst 1994), except where this is an uncommon physical feature (e.g., Yukon and se. NWT, 33% sites with overhangs; Platt 1977, Kuyt 1980). Substrate varies with area: in Alaska roughly half ledges shale, half sandstone or conglomerate (Cade 1960; White and Cade 1971); in NWT, diabase (Poole and Bromley 1988b). In taiga of se. and nw. NWT, > 60% of nests in white spruce (*Picea glauca*) in nests of Common Raven and Golden Eagle, 5–8 m above ground and 1–5 m below tree top (Kuyt 1962, 1980, Obst 1994); in w. Alaska nests have been documented in old Common Raven nests in balsam poplar (*Populus balsamifera*) (Kessel 1989). In Alaska, Gyrfalcons have also been recorded nesting on artificial structures, including trans-

Alaska oil pipeline, gold dredges, and sluice boxes (White and Roseneau 1970, Ritchie 1991).

Nest

Construction.

None to speak of. Not known to construct stick nests in North America, but reported to do so in Russian Arctic (Cade et al. 1998b). Both male and female scrape, which probably functions as much as a courtship ritual as "nest-building." Stick nests of other species usually not added to or modified. Stick nests often destroyed during course of raising young.

Structure and Composition.

Varies with species usurped; generally dead sticks, with little or no lining; eggs usually laid on bare soil or accumulated debris.

Dimensions.

Varies with species usurped; outside dimensions roughly 0.6–1.2 m deep and wide.

Microclimate.

Prefers sites not exposed to severe winds (Cade 1960). In Alaska, 62% of sites oriented northward (Cade 1960); in central NWT, no bias in orientation (Poole and Bromley 1988b, Obst 1994). In Yukon and se. NWT, most sites oriented south or west (Platt 1977, Kuyt 1980). This orientation may be preferable in sites lacking overhangs to keep them free of snow; snow-free sites not frequented preferentially during winter, but more likely to be occupied during nesting (Platt 1976). Young in nests with southern and western exposures; however, appear heat-stressed on sunny days (Fletcher and Webby 1977,

Poole and Bromley 1988b). No information on insulative value of stick nests relative to ledge nests.

Maintenance or Reuse of Nests, Alternate Nests.

Maintenance of stick nests dependent on other species. Between 1 and 3 alternative nest sites usually available within 1–1.4 km. Most, but not all, pairs change nest sites between years (Poole and Bromley 1988b, Nielsen and Cade 1990b, Obst 1994). Nest ledges reused over many years; carbon dating of accumulated feces at historical nest sites in Greenland revealed use over the past 2,500 years (The Peregrine Fund 2005b).

Nonbreeding Nests.

Not known to occur.

Eggs

Data in this section from The Peregrine Fund, unpublished, except where noted.

Shape.

Short elliptical.

Size and Mass.

Mean length, 58.46 mm (55.66–61.54 mm); mean breadth, 44.95 mm (43.19–48.01, $n = 2$ clutches, 7 eggs from Mackenzie, Canada; 3 clutches, 11 eggs from Labrador; Western Foundation Vertebrate Zoology [WFVZ]). Mean fresh weight of 52 first-clutch eggs from captive birds, 61.99 g ± 2.87 SD; captive eggs average 4% shorter and narrower than wild eggs, which translates to 8.9% difference in mass. Eggs approximately 3.5% of female body weight overall, but no reported values available for individual females. No

geographic variation in egg size. Egg size varies among clutches of different females, as does degree of variability (Poole and Bromley 1988b). In captivity, 1 egg (probably last laid) of 4-egg clutches generally smaller.

Color.

Overall appearance ranges from almost white to uniform reddish brown. Base color white or yellowish white; variably spotted with cinnamon.

Eggshell Thickness.

Mean thickness, with membrane 0.429 mm ± 0.016 (0.409–0.470, $n = 4$ clutches, 14 eggs from Canada; collected 1864–1904 [WFVZ]). Mean weight of empty shell, 5.981 g ± 0.474 (5.355–6.615 g, $n = 1$ clutch, 3 eggs from MacKenzie, Canada; $n = 2$ clutches, 3 eggs from Labrador) [WFVZ]). No geographic variation in eggshell thickness or weight. See also Conservation and Management: effects of human activity.

Egg-Laying.

Female becomes lethargic about 5 d before egg-laying. No information on time of day of laying for wild birds. Interval between eggs about 60 h (Platt 1977). In captivity, inter-egg interval decreases with subsequent eggs (Seifert 1982). As many as 13 replacement eggs laid by a single captive bird when eggs are pulled sequentially. Intraspecific egg-dumping not known to occur.

Incubation

Onset of Broodiness and Incubation in Relation to Laying.

No information on onset of broodiness for wild birds. Incubation typically begins with penultimate egg (Platt 1977) but may start sooner with onset of bad weather (TJC).

Incubation Patches.

Both male and female have 2 paired lateral brood patches, although male's are more poorly developed than female's (Cade 1982).

Incubation Period.

Incubation period 35 d for wild birds (n = 1), estimated at 35–36 d for 2 other nests (Platt 1977). Previous estimates of incubation period much lower, 28–29 d (Manniche 1910, Witherby et al. 1943, Cade 1960). Mean incubation period of captive birds 33.29 d ± 2.13 SD, n = 98, range 29–41, The Peregrine Fund). Incubation period 3–5 d longer for captive eggs from same clutch incubated artificially versus naturally (Seifert 1982).

Parental Behavior.

Both sexes incubate, but males participate only 17–24% of time (Poole and Bromley 1988b). Length of incubation bouts of females about twice as long as those of males (females, 260.6 min ± 148.6 SD; males, 140.1 ± 58.4 min); only females incubate through night. Male interest appears to decline during course of incubation period (Platt 1977). Eggs are left uncovered for 2–4 min when adults change places, although during a period of -35°C temperatures, change-over was accomplished in 20–45 s, with one bird sometimes lying down next to other prior to change. Female does not always allow male to take over incubation, giving agonistic Chatter with out-stretched neck. Birds approach scrape walking in a horizontal position; at scrape, steps are slow and high with feet loosely clenched. Feet are worked beneath eggs as body is lowered with rocking motion and jerking back of head with beak pointed downward. Head movement is also performed as intention movement prior to incubation. Settling movements are repeated at irregular intervals during incubation, with bird generally changing orientation 90°. Incubating birds may "rim" scrape by scraping substrate inward with beak and piling

pieces of debris nearby, creating a ridge around scrape surrounded by an area clear of debris (Platt 1977).

Hardiness of Eggs.

No specific information, but first and second eggs of clutch are left unattended in subzero and freezing temperatures for hours without apparent harm in both wild (Platt 1977, K. Poole pers. comm.) and captive birds (Seifert 1982).

Hatching

Data in this section from The Peregrine Fund, unpublished, except where noted otherwise.

Preliminary Events and Vocalizations.

In captivity, pipping of eggshell occurs 46.8 ± 15.1 h prior to hatching (n = 94). From time of pip, clicking noises can be heard coming from egg (presumably from contact between egg tooth and eggshell). A soft complaining call (similar to Beg Call) often made by chick during hatching, and can be elicited by imitating adult's Chup vocalization. No information on hatching in wild birds.

Shell-Breaking and Emergence.

About 17.8% of eggs produced in captivity hatch between 0600 and 0759 h. No captive eggs hatched between 0100 and 0359 h, but most of hatching uniformly distributed throughout rest of day and night (n = 101). Duration of hatching process (once chick has begun to turn in shell) approximately 30–45 min (C. Sandfort pers. comm.). In wild birds, 6 broods hatched within 48 h, 1 hatched within 72 h, and several broods appeared to have hatched over up to 6 d from estimates of chick ages (Poole and Bromley 1988b). Such extended hatching periods may result from incubation starting before penultimate egg in

very cold weather (K. Poole pers. comm.). In captivity, 8 complete clutches where all eggs were viable hatched over 95.6 ± 82.4 h (range 9.4–221.9 h).

Parental Assistance and Disposal of Eggshells.

No information on parental assistance. At least some, probably most, adults eat eggshells upon hatch (TLB). Addled eggs, however, are left in nest until ultimately crushed (K. Poole pers. comm.).

Young Birds

Data from The Peregrine Fund, unpublished, except where noted.

Condition at Hatching.

In captivity, hatch weight averages 52.1 g ± 3.7 SD (n = 96). No linear measurements available for hatchlings. Thick primary down uniformly distributed in feather tracts, except sparser in posterior-medial portion of ventral tracts. Bill pale horn in birds that develop gray plumage but ranging from blackish to nearly colorless, gape pink, iris black-brown, cere, tarsi, and feet bare, pale yellowish-pink. Color of first down varies in relation to color of future feathers: lightest birds have pure white down and colorless talons as hatchlings; darker birds have a dark wash on down of head and/or back and dark talons; darkest birds have jet black talons and beak tips. Chicks hatch with eyes open, slitlike at first; in captivity, egg tooth retained for at least first week. Young are able to sit up on tarsi very shortly after hatching to beg food from adults, but gaping is not oriented at this age. Hatchlings respond to vibration or sound by food-begging. Hatchlings can move around sufficiently to find warmth.

Growth and Development.

Weight of hatchlings doubles by about day 5. Second down begins to come in at day 8 in captive birds, emerging from its own follicles, not replacing 1st down as suggested by Dementiev (1960). First down-feathers are replaced in prejuvenal molt by emerging contour and flight feathers (TJC) During most rapid growth (6–27 d), females gain weight faster than males (59 g/d vs. 50 g/d, Poole 1989). Primary 7 emerges at about 11 d and grows in a linear fashion up to about 40–42 d, at about 2 mm/d (Poole 1989). No information on timing or sequence of emergence of contour feathers on different feather tracts, but young are down-covered until about 3 wk and feathered by about 5 wk. At < 1 wk of age, in 5°C weather, young often move partially out from underneath brooding female (Platt 1976). Completion of growth of flight feathers does not occur until after nest departure.

No observations of direct inter-sibling conflict though older nestlings compete for food. No specific information on timing of behavioral development. Young birds sleep lying down, by sitting on tarsi and lying forward on their ventral surface; feet may be extended out and back if nestlings are heat-stressed. When cold-stressed, sleep sitting up with head tucked, or seek out siblings. When older, also adopt adult sleeping postures, but generally prop themselves against some object. Gradually spend more time standing and less time sitting on tarsi. When able to stand, begin stretching (see Behavior: self-maintenance) and wing-flapping. Wing-flapping accomplished by leaning forward, grabbing substrate with feet, and flapping with wings held slightly above and behind back. Preening behavior begins before emergence of contour feathers. Young first fly at 45–50 d of age (Poole and Bromley 1988b) before flight feathers are hard-penned.

Parental Care

Brooding.

Brooding begins during hatching (Bente 1981). Young are brooded almost continually (> 80% of time) for minimum of 6 d (Platt 1977) and maximum of 19 d (Poole and Bromley

1988b), with 10–15 d most typical (Jenkins 1978, Poole and Bromley 1988b). Brooding time subsequently drops precipitously (Jenkins 1978), with young brooded only at "night," during rain showers, or briefly after feedings (Platt 1977). Brooding ceases completely as early as 11 d (Platt 1977) and as late as 27–32 d (Bente 1981, Poole and Bromley 1988b), with 16–25 d probably more typical (Jenkins 1978, Poole and Bromley 1988b). Male participation in brooding ranges from 0% (Platt 1977) to 5–25% (Jenkins 1978, Bente 1981, Poole and Bromley 1988b) and is greatest during first 5 d after hatching (Jenkins 1978). Brooding bouts of females averaged 43–97 min (Platt 1977, Bente 1981, Jenkins 1982); bouts of males about 28–54% of females', with up to 6 bouts/d total for both sexes (Bente 1981, Jenkins 1982). Brooding by male generally occurs while female feeds (Jenkins 1978). Female sometimes carries or drags young nestlings by mouth.

Feeding.

Feeding of chicks begins on day of hatch (Jenkins 1978, Poole and Boag 1988). Age when chicks begin to cast pellets unknown. Chicks able to stand on prey and pull it apart by 4 wk of age (Platt 1977), but female continues direct feeding (apportionment to chicks, not just delivery of food to nest) of chicks almost until fledging (Platt 1977, Jenkins 1978, Bente 1981).

Adults first deliver food to nest without feeding it to nestlings (indirect feeding) at 29–43 d; such deliveries account for only 6% of all feedings (Poole and Boag 1988). Males participate in only 2.3–9.1% of direct feedings (Jenkins 1982, Poole and Boag 1988, Booms and Fuller 2003b). Male supplies all prey (primarily via food transfer to female) for first 2–3 wk (73% overall, Poole and Boag 1988), at which time female begins to hunt (Platt 1977, Jenkins 1978, Poole and Boag 1988). Male delivery of food directly to nest (without transferring to female) varies from 0-62% of all prey deliveries (Jenkins 1982, Booms and Fuller 2003b). Type and size of food items same as those eaten by adults (see Food Habits), but up to 5 wk of age, ptarmigan are brought plucked, decapitated, and sometimes partially dismembered. By 6 wk, adults begin to bring

decapitated, partially plucked ptarmigan that are then plucked on ledge (Platt 1977). Male may first feed on prey away from nest (see Food Habits: food capture and consumption).

Delivery of prey either fairly uniform throughout day (Fletcher and Webby 1977, Bente 1981, Poole and Boag 1988), or exhibiting peaks in late morning and evening with a significant lull in very early morning (Jenkins 1982, Booms and Fuller 2003b). Feeding rates partially dependant on size of prey. Peaks at 10–12 d (maximum 12 feedings/d, Poole and Boag 1988) and 18–20 d (maximum 20 feedings/d, Bente 1981). Feeding rates decrease after 25–29 d (maximum 6–20 feedings/d, Bente 1981, Jenkins 1982, Poole and Boag 1988) unless diet shift to small prey occurs (Booms and Fuller 2003b). Feedings average 6–13 min in length (Bente 1981, Jenkins 1982, Poole and Boag 1988, Booms and Fuller 2003b), with average of 84–218 min between feedings (Fletcher and Webby 1977, Platt 1977, Bente 1981, Poole and Boag 1988). Feedings by males last about half as long as those by females (Jenkins 1982). Adults appear to be able to adjust prey biomass to number of young (Poole 1988b). Adults apportion food fairly evenly among chicks (Platt 1977, Bente 1981). At 15 d, when chicks begin to compete actively for food, distribution may become more skewed (Platt 1977). Although some have described behavior of chicks during feeding as aggressive (Jenkins 1978), and chicks may or may not mob adults at feedings, no sibling aggression observed, even at ages near fledging (Platt 1977, Bente 1981). Degree of aggressiveness may relate to food availability as seen in other raptor species.

Nest Sanitation.

Young defecate by backing away from center of scrape, bending forward as if stretching, and directing a stream of urine and fecal material away from scrape (Jenkins 1982). No information on frequency of excretion. Use of traditional nest ledges can cause excrement and nesting debris to become several meters deep over time (Burnham and Mattox 1984). Adults remove 0-21% of prey remains from nest after feedings (Platt 1977, Booms and Fuller 2003b). For information on invertebrates associated with nest sites, see Demography and Populations: diseases and body parasites, and causes of mortality.

Cooperative Breeding

Not known to occur.

Brood Parasitism

Not known to occur, although stray Canada Goose and Rough-legged Hawk eggs have been found in Gyrfalcon nests (TJC).

Fledgling Stage

No information on mass or linear measurements at fledging, though fledglings appear similar to adults in all but feather growth and mass. In the Northwest Territories, fledglings remain within 200–300 m of nest for 7–10 d. By week 2 they travel up to 1 km, still returning to nest regularly. By 20 d post-fledging, some young have moved from general vicinity of nest (Poole and Bromley 1988b). Fledglings associate with adults and siblings during fledgling stage, continuing to receive food from parents (Platt 1976, Fletcher and Webby 1977, Bente 1981).

Immature Stage

Little information. Immature birds become independent of parents 4–6 wk after fledging. Groups of birds sighted in fall are suggested to be comprised of immatures (Cade 1960, Platt 1976). Immature birds prey heavily on rodents, passerines, and young ptarmigan (Cade 1982). No evidence of immatures remaining on breeding territories during winter (Platt 1977, Nielsen and Cade 1990b) and no directional trends of post-fledging movements observed (Britten et al. 1995).

DEMOGRAPHY AND POPULATIONS

Measures of Breeding Activity

Age at First Breeding.

In Iceland, age at first breeding for one female was 2 yr, age at first breeding for one male was 4 yr (Nielsen and Cade 1990b). In captivity 3 pairs of birds with like-aged mates bred at 2 yr, 3 yr, and 4 yr of age (The Peregrine Fund) and Seifert (1982) had 1 pair that bred when female was 4 yr and male was 3 yr. Suggestion that Palearctic birds may occasionally breed in first year considered unlikely (Dementiev and Gladkov 1957, Cramp and Simmons 1980). Pairs do not necessarily attempt breeding every year (Cade 1960, Nielsen and Cade 1990b). Interval between breeding years varies and is dependent on food supply (Nielsen and Cade 1990b).

Clutch.

Mean clutch size 3.72 ± 0.71 (range 1–5, n = 122 clutches from Alaska, Labrador, Greenland, and Iceland [WFVZ]). No geographic variation in clutch size documented, although clutch size declines as breeding season progresses (Barichello 1983). See also Cade et al. (1998a) and Potapov and Sale (2005) for data outside North America.

Annual and Lifetime Reproductive Success.

Over a 10-yr period in the Northwest Territories (NWT), Canada, 54% of territories were occupied each year, on average (Shank and Poole 1994). Over a 4-yr period in NWT, 23% of pairs occupying territories did not lay eggs (Poole and Bromley 1988b). Estimated combined egg and nestling mortality was 48%, giving overall annual productivity of 1.5 young/active nest (Poole and Bromley 1988b). Brood size averaged 2.54 young over 10-yr period over entire NWT; no temporal or spatial trends observed in brood size (Shank and Poole 1994). Little difference observed between brood size at first sighting and brood size at fledging, indicating most mortality takes place either at egg

stage or early in nestling period (Cade 1960, Nielsen 1986). Over 10-yr period, however, 73.6% of occupied territories (43% of available territories) in NWT produced young (Shank and Poole 1994), so relatively small proportion of pairs fail completely.

Of 2 copulating captive females, paired as young birds and retained until their death, 1 produced 97 eggs with 47% fertility, 70% of which hatched; the other produced 90 eggs with 63% fertility, 79% of which hatched. Eggs and clutches were removed from these birds throughout the breeding season each year, so numbers represent maximal productivity (The Peregrine Fund). Fertility rates in captivity probably lower than in wild birds.

Life Span and Survivorship

Oldest wild bird recovered in Iceland was 12 yr old male (Cade et al. 1998a); in the NWT, a banded female (re-sighted) believed to be 12 yr old, assuming age at 1st breeding was 3 yr (K. Poole pers. comm.). Three captive females averaged 12 ± 4.6 yr at death (The Peregrine Fund). Of 46 recovered birds banded as nestlings, 67.4% were juveniles, 93.5% were either juveniles or subadults (Nielsen and Cade 1990b). Of another 38 birds found dead or diseased in Iceland, 84% were < 1 yr old (Clausen and Gudmundsson 1981). Little survivorship data from N. America, but breeding adult survival estimated at 90% in Iceland; no information on first year survival, but possibly around 50% (Cade et al. 1998a).

Disease and Body Parasites

One nestling in the Northwest Territories succumbed to an infestation of parasitic fly *Protocalliphora avium* at 10 d of age; infestations of dipteran larvae and fleas also observed (Poole and Bromley 1988b). Mosquitoes can also cause distress to young (TJC). Several nymphal ticks (*Ixodes howelli*) collected from 11 d old nestlings in Alaska (White and Springer 1965). In Iceland, nematode *Capillaria contorta* found in 36 of 38 birds; 13 birds died from these infestations, remainder only lightly affected. Small

numbers of other parasites found in intestines in 12 out of 38 birds: *Hymenolepis* sp. (7), *Plagiorchis elegans* (2), *Cladotaenia cylindracae* (2), and *Mesocestoides* sp. (1) (Trainer et al. 1968, Clausen and Gudmundsson 1981). No hematozoa observed in the blood of 2 Greenland Gyrfalcons (Taft et al. 1998).

In Iceland, 8 of 13 birds dying from parasitic infections also had pneumonia. *Corynebacterium murium* isolated from 1 bird and *C. pyogenes* from another (Clausen and Gudmundsson 1981). Nonclinical bacterial isolates from wild birds include *Escherichia coli*, *Streptococcus* sp., *Staphalococcus epidermis*, *Haemophilus aphrophilus*, *Proteus mirabilis*, *P. vulgaris*, and *Actinobacillus* sp. (Cooper et al. 1980). Captive birds susceptible to avian cholera (*Pasturella multocida*, Williams et al. 1986), avian malaria (*Plasmodium relictum*), Aspergillosis (*Aspergillus fumigatus*), frounce (*Trichomoniasis gallinas*) (Hamilton and Stabler 1953), and pigeon herpes, with all being potentially fatal. Aspergillosis and West Nile virus most serious infections of captive Gyrfalcons (TJC). Nonclinical presence of *Staphalococcus* sp., non-hemolytic *Streptococcus* sp., and various gram-negative bacteria observed in captive birds.

Causes of Mortality

Weather probably a major cause of mortality in nest; snowfall negatively correlated with number of young per occupied nest (Nielsen 1986, Poole and Bromley 1988b), and nest abandonment often associated with, and attributed to, isolated events of severe weather. Nest sites with northern orientation may have higher success than those with southern orientation (Barichello 1983, Poole and Bromley 1988b; see Nest: microclimate). Starvation of nestlings also occurs (Cade 1960, Poole and Bromley 1988b). No record of predation on nestlings by other species.

Of 23 birds found dead out of the nest in Iceland, 8 (35%) were hit by cars, 7 (30%) hit other objects, 4 (17%) were shot, 2 (9%) were oiled, and 2 were found emaciated (Nielsen and Cade 1990b). Of 38 unbanded birds found dead or diseased in Iceland, 13 (34%) died from parasitic infections, 12 (32%) were shot, 8 (21%) died of trauma, 2 (5%) were oiled, 2 died of unknown causes, and 1 (3%) was poisoned (Clausen

and Gudmundsson 1981). Several birds in se. Northwest Territories poisoned by strychnine-loaded caribou carcass (Kuyt 1980). Human-related causes of mortality may be lower in North America, where Gyrfalcon populations are more isolated.

Range

Initial Dispersal from Natal Site.

No information on natal dispersal or philopatry in North America. In Iceland, two males found breeding 14 and 25 km from their natal site; two females bred 53 and 84 km from natal site (Nielsen 1991).

Fidelity to Breeding Site and Winter Home Range.

Nest sites are traditional and may be used for generations, but little information on fidelity of individuals. Generally thought to be site faithful. In Iceland, 2 banded females remained faithful to sites for 3 and 4 yrs (Nielsen and Cade 1990b) and in w. Alaska, 1 banded female remained faithful to site for at least 3 yrs (TLB unpub. data). Maximum known number of consecutive years for site occupation is 5 yrs (Burnham and Mattox 1984, Poole and Bromley 1988b). One banded female in NWT observed 10 yrs later on same territory, although fidelity to this site may not have been continual (K. Poole pers. comm.). In South Dakota, 1 subadult female established winter home ranges with > 50% overlap in 2 consecutive yrs (Sanchez 1993).

Dispersal from Breeding Site.

Almost no information in North America; one banded breeding female bred 5 km (in a different historical territory) from nest where captured (TLB unpub. data). Breeding females recaptured in Iceland in same territory and within 5.9 km of previous nests (Nielsen 1991).

Home Range.

One female with older nestlings remained within 3.2 km of eyrie during all activities; the male patrolled an area of about 200 km^2, at one point traveling up to 24 km from nest site. Range size probably varies annually and geographically with prey abundance (White and Nelson 1991). One breeding female harnessed with a satellite transmitter in Greenland ranged over 589 km^2 (Klugman et al. 1993). All radio-tagged wintering subadults in South Dakota ($n = 4$) established home ranges; mean maximum home ranges were 4,422 ± 956 km^2, high-use areas (85% harmonic mean) averaged 1,586 ± 263 km^2, and average range length was 32.3 ± 6.1 km. Two birds with adjacent ranges shared only 5–7% (247 km^2) of their ranges, and another 2 had ranges with no overlap (Sanchez 1993). Range lengths of immatures averaged longer than those of subadults ($n = 5$, 94.9 ± 31.7 km) and generally showed little reuse of area. One immature did appear to set up a home range south of his study area (Sanchez 1993), and 1 immature in Washington established a home range similar in size to that of sub-adults in South Dakota (Dobler 1989).

Population Status

Numbers.

Alaska. (White and Springer 1965, Roseneau 1972, Swartz et al. 1975, Swem et al. 1994). Total known pairs about 180, estimated pairs about 375–635; north (northern slope Brooks Range and Arctic slope), about 90 pairs known at 1/181 km^2, up to 9 in 38 km along rivers with suitable cliffs; west (between Brooks Range and Alaska Peninsula), about 56 pairs known, estimated about 132 pairs at 1/176 km^2–1/1,000 km^2; central (Alaska Range, Wrangell Mtns., southern slope Brooks Range), about 26 pairs at 1/212 km^2, largest region, most not surveyed; southwest (Aleutians and Alaska Peninsula), about 6 pairs known, estimated about 36 pairs; south/southeast (Gulf of Alaska and Pacific Ocean), about 3 pairs known, estimated about 30 pairs.

Yukon. (Mossop and Hayes 1994). Total known pairs about 240, estimated about 748, total estimated population 2,490–4,180 birds; North Slope, about 106 pairs known in 17,500 km^2 at 1/165 km^2, nearest neighbor distance 8.1 km, estimated about 188 pairs in 31,020 km^2; southern Richardson Mtns., about 17 pairs known in 15,947 km^2 at 1/1,724 km^2, nearest neighbor distance 18.2 km, estimated about 90 pairs in 85,200 km^2; Ogilvie Mtns., about 58 pairs known in 17,302 km^2 at 1/299 km^2, nearest neighbor distance 11.0 km, estimated about 184 pairs in 54,903 km^2; Dawson Range, about 10 pairs known in 5,030 km^2 at 1/505 km^2, nearest neighbor distance 25.6 km, estimated about 155 pairs in 78,450 km^2; Kluane Range, about 6 pairs known in 10,227 km2 at 1/1,695 km^2, estimated about 11 pairs in 18,906 km^2; Macmillian Pass, about 7 pairs known in 10,965 km^2 at 1/1575 km^2, nearest neighbor distance 96.7 km, estimated about 28 pairs in 42,436 km^2; Coast Mtns., about 36 pairs known in 10,023 km^2 at 1/279 km^2, nearest neighbor distance 12.4 km, estimated about 92 pairs in 25,550 km^2.

Northwest Territories. (Shank and Poole 1994). Estimated total pairs about 1,300, estimated total population about 5,000 birds; Queen Elizabeth I., estimated about 45 pairs in 17,000 km of coastline at 1/375 km of coast, mean internest distance 75 km; Low Canadian Arctic I. estimated about 175 pairs in 26,000 km of coastline at 1/150 km of coastline, mean internest distance 50 km; mainland coast, estimated about 195 pairs in 8,500 km^2 at 1/175–1/875 km^2; mainland interior, estimated about 450 pairs in 900,000 km^2 at 1/2,000 km^2; Mackenzie and Richardson Mtns., estimated about 425 pairs in 150,000 km^2 at 1/350 km^2.

British Columbia. Fifteen breeding locations known, south to 57° 45' N (Campbell et al. 1989).

Quebec. S. Quebec, about 15 pairs known; Ungava, about 35 pairs known; Hudson's Bay coast and nw. islands, about 5–10 pairs known; n. Quebec, estimated population > 1,000 birds (M. LaPage pers. comm.). Most of Hudson Bay islands and much of mainland unsurveyed.

Labrador. 10–12 known pairs; estimated population much higher; surveys not conducted specifically for this species (J. Brazil pers. comm.).

Greenland. Koskimies (2006a) estimates 500-1,000 pairs, though many areas remain unsurveyed.

North America. Approximately 3,400 to 4,300 nesting pairs, based on estimates above; 2,925 to 3,875 more recently estimated (Potapov and Sale 2005). No information on size or status of non-breeding population.

Worldwide. Former estimate of 15,000–17,000 pairs (Cade 1982) too high based on overestimated range of 15–17 million km^2); recent country by country estimates yield total of 7,880 to 10,900 breeding pairs (Potapov and Sale 2005). No information on non-breeding population.

Trends.

No evidence of long-term population changes in North America (Fyfe and Grier 1972, Cade 1982, Mossop and Hayes 1994, Shank and Poole 1994, Swem et al. 1994), except for s. coast of Labrador and adjacent Quebec, where Gyrfalcons may have been more common breeders during the Little Ice Age, which did not end until mid-1800s (Audubon 1897, Townsend and Allen 1907); however, most of Nearctic range has not been surveyed or monitored. Some historical losses noted in Scandinavia (Cade et al. 1998a), but see Koskimies (2006b).

Population Regulation

Breeding population size limited by presence of suitable nest sites and sufficient prey (Shank and Poole 1994). Size of breeding populations fluctuates widely among years (Swartz et al. 1975, Platt 1977, Nielsen 1986, Mossop and Hayes 1994, Swem et al. 1994). Population changes irregular, i.e., not cyclic in some areas (e.g., Alaska, Mindell et al. 1987, Mindell and White 1988, Swem et al. 1994) but cyclic in others (e.g., Yukon, Mossop and Hayes 1994). Size of breeding population correlated with ptarmigan numbers in most populations (Mossop and Hayes 1982, 1994, Nielsen 1986). In Iceland, total number of Gyrfalcons present in late summer and number of occupied territories

were correlated with ptarmigan density with a 2 and 3-year time lag, respectively (Nielsen 1999). Reproductive success of individual nests mimics trend in population size (i.e., higher when occupancy is higher) in some areas (Mossop and Hayes 1994) but not in others (Mossop and Hayes 1982, Nielsen 1986, Shank and Poole 1994, Swem et al. 1994). Conflicting trends may reflect geographic variation in temporal stability of ptarmigan populations (Mossop and Hayes 1982) or availability of alternative prey (Mossop and Hayes 1994).

Specialization of Gyrfalcons on ptarmigan does not appear to influence ptarmigan population levels in some regions (Gudmundsson 1972). In Iceland, however, Gyrfalcon and ptarmigan numbers regularly fluctuate in a 10-yr cycle (Nielsen and Pétursson 1995), and Gyrfalcons influence the ptarmigan cycle by accelerating population declines, accentuating the amplitude of the cycle, and affecting the duration of the low periods of the cycle (Nielsen 1999). This suggests Gyrfalcon predation causes the ptarmigan population cycles in Iceland (Inchausti and Ginzburg 2002) and likely influences the cycles in Sweden (Nyström et al. 2006).

Reproductive success and timing are related to weather (Nielsen 1986, Poole and Bromley 1988b), but weather is not correlated directly with size of breeding population (Poole and Bromley 1988b). Geographic trends in population density correlate with higher summer temperatures and taller willows, which may reflect relative productivity of habitat (Shank and Poole 1994) and availability of winter cover for ptarmigan. Although sizes of local breeding populations vary annually, there is no indication that the Gyrfalcon population as a whole responds in similar manner.

Although Gyrfalcons have breeding requirements similar to those of Peregrine Falcons, Rough-legged Hawks, Golden Eagles, and Common Ravens, there is no evidence that interspecific competition influences size of Gyrfalcon breeding populations or their reproductive success (Cade 1960, Poole and Bromley 1988a). Conversely, these other species provide potential nest sites for Gyrfalcons. Sites where pairs depend on stick nests may be occupied less frequently than ledge sites because young Gyrfalcons destroy much of nest, requiring a renesting attempt by other species to maintain it

(Burnham and Mattox 1984). Use of some nest sites by Gyrfalcons and other species in alternate years has been observed in Alaska (White and Cade 1971, Swem et al. 1994) and NWT (Poole and Bromley 1988a). Intraspecific competition may be important; in NWT, Gyrfalcons nesting close to each other have lower reproductive success than pairs nesting farther apart (Poole and Bromley 1988a).

CONSERVATION AND MANAGEMENT

Effects of Human Activity

Not particularly aggressive when humans intrude on nest site, often slipping away and circling silently, though individual birds vary in degree of aggressiveness (Cade 1982). Some pairs become habituated to presence of humans on foot, at least at distances of 300 m (Platt 1977, Poole and Bromley 1988b). Improper approach to nest, however, can cause exposure, injury, or death of nestlings (Bromley 1986). In Yukon, birds were always disturbed by helicopter overflights at 150 m above nest site, less frequently disturbed at 300 m, and not disturbed at 600 m; birds were more disturbed by lateral approaches than approaches from above (Platt 1976); may attack fixed-wing aircraft (C. M. White pers. comm.). Disturbance from overflights did not result in abandonment or reduced productivity, but disturbed birds were less likely to reuse same nest site following year (Platt 1977).

Gyrfalcons may be negatively affected by radio and satellite backpack transmitters. One adult female temporarily abandoned its nest and regularly fought with its harness for a week after transmitter deployment, though it successfully fledged young (TLB). Of 11 fledglings and 3 breeding adults harnessed with approx. 30-g transmitters in w. Alaska, none were detected alive the following breeding season except for one adult that had removed its transmitter harness. One adult and 1 fledgling were confirmed dead the spring after deployment; fates of the remaining birds unknown (TLB unpub. data). No definitive data available on effects of transmitters on Gyrfalcons, but scant information available and field observations of harnessed birds suggests birds negatively affected.

Although shooting is a significant cause of mortality in Iceland (Clausen and Gudmundsson 1981, Nielsen and Cade 1990b), there is no information on the incidence of shootings in North America; presumably there would be fewer as North American Gyrfalcon populations are more isolated from human populations (Shank and Poole 1994). Little mortality caused by accidental capture in ptarmigan or fox traps in N. America, although this appears to be a significant source of mortality in Russia (Orden and Paklina 2000, Potapov and Sale 2005).

DDT contaminant levels were generally low in North American Gyrfalcons, almost an order of magnitude lower than those of arctic Peregrine Falcons, although levels of some individuals approached those of Peregrines (Cade et al. 1971, Walker 1977). Because most Gyrfalcons are resident, live in areas remote from pesticide use, and feed on non-migratory prey, they are generally less susceptible to contamination than the migratory Peregrine. Eggs and lipids of Alaskan Gyrfalcons contained both DDE (0–290 ppm) and PCBs (5.7–210 ppm) (Cade et al. 1971, Walker 1977). Eggs of birds from Northwest Territories (NWT) contained low levels of DDT, DDE, PCBs, oxychlordane, dieldrin, heptachlor epoxide, and aroclor 1254/126 (Bromley 1986, Poole and Bromley 1988b). Levels of DDE and PCBs in tissues of resident prey species insufficient to account for higher levels of contaminants observed in some individuals. Migratory prey species such as shorebirds had 10–100 times contaminant levels of resident species and probably account for higher levels of contaminants in some individuals (Walker 1977). In Greenland, where both predator and prey are resident, DDE was the only contaminant found in plasma; not found in all samples, and occurred at lower levels (< .02 ppm wet weight; Jarman et al. 1994). Icelandic ptarmigan had low levels of organochlorine contamination compared to migratory or marine-associated avian prey species (Olafsdottir et al. 2001). No eggshell thinning or other effects on reproduction noted (Cade et al. 1971, Walker 1977).

Gyrfalcon mercury levels in Europe (1.72 ± 3.35 ppm) also lower than in Peregrine Falcons (17.6 ± 6.99 ppm). Mercury levels higher in migratory (aquatic) prey, particularly shorebirds, and in Gyrfalcon nestlings fed a greater proportion of aquatic

species (Lindberg 1984). Lower levels of platinum group elements and organochlorines in Gyrfalcons compared to other raptors in Europe as well (Herzke et al. 2002, Jensen et al. 2002, Ek et al. 2004). Gyrfalcons in Greenland had lower mercury levels than Peregrine Falcons or White-tailed Eagle (Dietz et al. 2006). Overall, Gyrfalcons have low levels of contamination; those consuming migratory, marine-feeding, or insectivorous avian prey have higher contaminant loads than those relying on resident ptarmigan populations.

Habitat modification, egg collection, and falconers have all been blamed for population declines in Scandinavia and adjacent portions of Finland and Russia (Cramp and Simmons 1980, but see Cade et al. 1998a for evaluation), and removal of wild birds to commercial markets may threaten some populations in Russia (World Working Group on Birds of Prey 1992, Potapov and Sale 2005). Remoteness of breeding sites in North America has prevented such factors from negatively influencing these populations. Human populations and Gyrfalcon populations are not necessarily incompatible, however, as shown by high density of birds in Iceland, where the breeding population endured a loss of about 25% of its annual population (owing to export of birds to Europe) in prior centuries without long-term decline, and where much of habitat is overgrazed (Cade 1982, Nielsen and Pétursson 1995).

Most significant current and likely future effects of human activity on the Gyrfalcon are those of global warming. Although research in this field is just beginning and the current effects on Gyrfalcons can only be surmised by correlations (The Peregrine Fund 2005a), birds and other fauna are extending their distributions northwards and spring events are occurring earlier in concordance with documented climatic warming (Thomas and Lennon 1999, Parmesan and Yohe 2003, Hitch and Leberg 2007). The tundra landscapes to which Gyrfalcons are adapted are undergoing habitat change through shrub expansion in Alaska, Canada, and likely across the circumpolar Arctic (Sturm et al. 2001, Tape et al. 2006). From 1949 - 1998, mean annual temperatures in Alaska have increased up to 2.2° C (Stafford et al. 2000). The Gyrfalcon will likely be affected by these changes through numerous direct and indirect pathways. Likely

candidates include range constriction, changes in diet and breeding phenology, shrinking foraging habitats, thermal stress, increased human access to and disturbance of nests, extreme weather events affecting survival and nesting, and interspecific competition.

Management

No active management in North America. A few independent, long-term monitoring projects in parts of Greenland, Canada, and Alaska, though not coordinated.
The Gyrfalcon is protected in both Canada and the U.S. but is not listed as endangered or threatened. Because of the species' use in falconry and its associated value in foreign markets, however, its status has been controversial. North American populations were initially listed under Appendix I of C.I.T.E.S. (normally reserved for endangered species; prohibits import and export for commercial purposes) but were moved to Appendix II in 1981. In 1985, despite Canadian opposition, they were moved back to Appendix I in response to a proposal by Norway and Denmark, which had noted declines in Palearctic populations (Parrish and White 1987). Management of North American falcons is under state and provincial jurisdiction, but in Canada's 4 western provinces and 2 territories it is coordinated through the Western Raptor Committee, comprised of representatives from wildlife agencies from each jurisdiction.

There have been two Canadian attempts to manage the Gyrfalcon as a renewable wildlife resource for use in falconry: in the Yukon (Mossop and Hayes 1982) and in the Northwest Territories (Bromley 1986). Although biologically justifiable, these programs have met with limited success owing to political difficulties. Meanwhile, captive propagation has provided an increasing number of Gyrfalcons for falconry. Since the first Gyrfalcons produced by The Peregrine Fund at Cornell University in 1974 (Cade 1986), many hundreds of Gyrfalcons have been reared by a number of private breeders in Canada and the U.S., and many more in Europe. Most Gyrfalcons now flown in North American falconry are captive-produced birds. Legal, regulated harvest of wild-caught immatures, however, does occur, for noncommercial use only, in several states/provinces and likely has little or no impact on population viability.

APPEARANCES

(see also Systematics: Geographic Variation) Gyrfalcons have 10 functional primaries, 13 secondaries (including three tertials), and 12 rectrices. Plumage aspect varies extensively across large geographic areas (see Johnson et al. 2007), with "white," "gray/intermediate" and "dark" variants (see below). No geographic variation in molt strategies has been reported.

Molts

Molt and plumage terminology follows Humphrey and Parkes (1959) as modified by Howell et al. (2003, 2004). Gyrfalcon exhibits a Modified Basic Strategy (Howell et al. 2003), including complete prebasic molts and a limited preformative molt in some individuals (Pyle 2005a), but no prealternate molts (Cramp and Simmons 1980; Forsman 1999; Wheeler 2003a, 2003b; Pyle 2008; Fig. 4). The second prebasic molt typically results in definitive plumage aspect, although some juvenal and/or formative feathers can be retained through the second cycle.

Prejuvenile (First Prebasic) Molt.

Complete, Jun-Jul, in the nest. Primary 7 emerges at about 11 d and grows in a linear fashion up to about 40–42 d, at about 2 mm/d (Poole 1989). No information on timing or sequence of emergence of contour feathers on different feather tracts, but young are down-covered until about 3 wks and feathered by about 5 wks. Completion of growth of flight feathers does not occur until after fledging.

Preformative Molt.

Absent to limited, Nov-Mar, primarily on non-breeding grounds. Can include up to 30% of body feathers but appears to be absent in most individuals (Pyle 2005a, 2008). No wing coverts or flight feathers replaced.

Second Prebasic Molt.

Incomplete to complete, Mar-Sep, primarily on breeding grounds (although individuals not breeding during this cycle). Molt continuous without suspensions. Retention of feathers as in Definitive Prebasic Molt (see below) perhaps less common due to lack of energy constraints related to breeding. Dementiev (1960) suggested that birds undergoing their Second Prebasic Molt may begin body molt in winter and replace flight feathers in spring but this likely based on preformative molt followed by beginning of prebasic molt (*cf.* Pyle 2005a).

Definitive Prebasic Molt.

Incomplete to complete, Apr-Oct, on breeding grounds (Dementiev 1960, Cramp and Simmons 1980). Primaries and secondaries each replaced both distally and proximally, from centers at p4-p5 and s5 (Miller 1941, Pyle 2005b); e.g., typical sequence of primaries 4–5–6–3–7–2–8–9–1–10. Reports of initiation at p3, p6, or p7 (Waller 1939, Dementiev and Gladkov 1957) require confirmation. Duration of primary molt 98–127 d (Cramp and Simmons 1980) to approximately 150 d in captive birds (TJC). Tertials molt outward in sequence to meet proximal replacement wave beginning at s5 (Palmer 1988). Rectrices generally replaced distally on each side of tail but r6 usually replaced before medial rectrices; typical sequence 1–2–3–4–6–5 or 1–2–6–3–4–5. Duration of rectrix molt 75–84 d (Cramp and Simmons 1980) to approximately 100 d in captive birds (TJC).

A period of down molt precedes molt of contour feathers and then stops; a second period of down molt occurs at end of body molt. Uncertain whether these 2 episodes of down replacement represent full or partial down molts (TJC). Early replacement of down

may be related to brooding young in cold climates; later replacement (during hot weather) may facilitate thermoregulation (Palmer 1988).

Molt of pennaceous feathers begins with primaries and rectrices; secondaries and body feathers follow soon after. In breeding individuals molt can begin during incubation and suspend for chick-feeding after 1-4 medial primaries (among p3-p6), 1-3 medial ss (among s4-s6) and the tertials nave been replaced; molt averages earlier commencement and more feathers replaced before suspension in females than males. No captive birds have been observed to interrupt molt during breeding; on the contrary, if a bird is going to breed, even very late in the season, molt will be delayed; likewise early molt is an indication a bird will not breed in captivity. Scattered wing coverts, body feathers (especially on rump), and occasionally p10 and/or s1 can rarely be retained (Dementiev and Gladkov 1957, Johnsgard 1990, Sanchez 1993, Pyle 2008; TJC); retention perhaps more common in successful breeders due to energy constraints. Reports that juvenal feathers can be retained through third cycle unlikely and require confirmation.

Plumages

See Dementiev and Gladkov (1957), Friedmann (1950), Roberts (1955), Cramp and Simmons (1980), Palmer (1988), Cade et al. (1998a), Forsman (1999), and Wheeler (2003a, 2003b) for detailed plumage descriptions. Following taken from these and Williams and Matteson (1948), Brown and Amadon (1968), Potapov and Sale (2005), and examination of 68 North American study skins, and 14 live or recently-dead birds by Clum and Cade (1994). Color terminology follows Smithe (1975). All colors observed on Gyrfalcons fall in yellow/yellow-red continuum; all colors tend to be of moderate value (3–7) and poorly saturated (< 4.0). Plumages of all birds contain 2 basic colors: a lighter "background" color and a darker "marking" color resulting in streaks, spots, or bars on feathers. In their quantitative study of plumage coloration in the Gyrfalcon, Potapov and Sale (2005) found no feathers that reflect in the ultra-violet range of the spectrum.

The Gyrfalcon shows extreme variation in plumage color and pattern, exhibiting a range from almost uniform white to uniform brownish-black. Intermediate plumages

form a continuous gradation between the two extremes with no distinct breaks or divisions. Although not uniformly agreed upon (see Potapov and Sale 2005), use of terms that describe distinct, identifiable color patterns such as "morph" or "polymorphism" for Gyrfalcons is incorrect (Cade et al. 1998a, Flann 2003, Cade 2006) and misleading. For convenience, most birds are lumped into one of three generalized descriptors: white, gray/intermediate, and dark "variants". Each group is described in terms of a range of patterns and colors. White variants have a large proportion of background color to marking color; reverse is true for dark variants; gray/intermediate variants have intermediate amounts of both. The change in proportions results from changes in length and width of shaft-streaks on spotted and streaked feathers (generally on head and ventral body surfaces) and in completeness of barring on barred feathers (generally on mantle, wings, tail, and legs). In complete barring, dark bars are continuous from one lateral edge of feather to the other with bands of light background color between; in incomplete barring, background color on either side of shaft is interrupted in middle by darker marking color. Juveniles and adults, as well as males and females, show differences in proportions of background to marking colors. Adults have smaller or no shaft-streaks on breast, belly, and head, compared to immatures. Ventral surfaces more likely to be spotted and barred rather than streaked; immatures always streaked. Males generally less heavily marked on ventral surfaces, but females often have lighter markings on head.

Natal Down.

(May-Jul) uniformly distributed in feather tracts, except sparser in posterior-medial portion of ventral tracts. Color of first down varies in relation to color of future feathers: lightest birds have pure white down and darker birds have a dark wash on down of head and/or back. Second down is lighter in color and denser than 1st and begins to come in at day 8 in captive birds. It emerges from different follicles than 1st down; pinnaceous feathers later erupt from these same follicles, the second down adhering to the feather tips. Young are down-covered until about 3 wks and feathered by about 5 wks.

Juvenal Plumage.

(Aug-Jul). Juvenile primaries are thinner and more tapered, and have rounder bars (oval-shaped), when present, than definitive primaries. Juvenile rectricies are narrower and more tapered than definitive rectrices (Pyle 2008).

White variants with background color overall white to a dilution of pale horn color (92). Forehead, crown, and nape finely streaked with Van Dyke brown (121); mantle moderately to heavily marked, having feathers incompletely barred olive brown (28) to sepia (119) with arrowhead tips of same color and broad light margins both terminally and laterally; breast and belly lightly to moderately streaked with Van Dyke brown teardrops; tail clear or lightly to heavily barred olive brown to sepia; primaries with broad irregular subterminal band Van Dyke brown to sepia, variably barred with same color on inner web; secondaries incompletely barred with olive brown to Van Dyke brown; axillaries and underwing coverts with Van Dyke brown shaft-streaks or arrowheads.

Gray/intermediate variants with forehead, crown, nape, and cheeks pale horn color heavily streaked with olive brown to Van Dyke brown; nape sometimes with conspicuous ocelli (eye-like patches) of pale horn; weak facial stripe of Van Dyke brown; mantle pale horn color (occasionally salmon, 6) almost completely barred with olive brown to Van Dyke brown; breast and belly pale horn color moderately streaked with olive brown to Van Dyke brown; tail pale horn to light neutral gray heavily to moderately barred with olive brown or Van Dyke brown, dark marking color sometimes surrounds spots of pale background color (similar to Saker Falcon); primaries pale horn with irregular Van Dyke brown to sepia incomplete barring; secondaries pale horn incompletely barred olive brown to Van Dyke brown; axillaries and underwing coverts barred olive brown to Van Dyke brown with pale horn color margins and spots.

Dark variants with forehead, crown, nape, mantle, and cheeks uniformly Van Dyke brown, sometimes with darker shafts; breast and belly pale horn heavily streaked with olive brown to Van Dyke brown; tail light neutral gray (85) strongly barred with olive brown to Van Dyke brown or uniformly Van Dyke brown; primaries pale horn

color with heavy irregular Van Dyke brown to sepia bars on inner webs, and leaving pale horn color spots or speckles on outer webs; secondaries pale horn color heavily barred olive brown to Van Dyke brown; axillaries and underwing coverts heavily barred olive brown to Van Dyke brown leaving minimal pale horn margins and spots.

Second Basic Plumage.

(Sep-Aug). Aspects like that of Definitive Basic Plumage (below) but one to a few juvenile wing coverts and/or body feathers (especially on rump) retained, worn, and showing patterns of juvenile feathers. Rectrices and body markings sometimes intermediate in pattern between juvenile and definitive basic patterns. Primaries and secondaries showing even molt clines, (i.e., without "suspension limits"; Pyle 2008).

Definitive Basic Plumage.

(Sep-Aug). Definitive basic primaries are broader and more truncate at tip, and have squarer bars, when present, than juvenal primaries. Definitive rectricies are broader and more truncated than juvenal rectrices (Pyle 2008). Individuals in their 3rd cycle or later can be identified by the retention of feathers, as in Second Basic Plumage, but retained feathers proportionally less worn and showing shapes and patterns of definitive feathers. Markings also not intermediate and in some cases (e.g., in extremely white variants) may in certain cases be diagnostic of older individuals but more study is needed.

White variants with background color white; forehead, crown, nape, and cheeks clear to finely streaked with sepia; mantle lightly to heavily marked, having feathers subterminally spotted to completely barred with sepia; breast and belly clear to lightly marked with small sepia teardrops; tail clear or subterminally spotted to strongly barred with sepia; primaries with broad irregular sepia subterminal band, incompletely barred with sepia on inner web; secondaries incompletely barred with sepia; axillaries and underwing coverts clear to lightly marked with sepia shaft-streaks.

Gray/intermediate variants with forehead, crown, nape, and cheeks white to pale horn color lightly to heavily streaked with dark neutral gray (83); nape sometimes with conspicuous ocelli (eye-like patches) of white to pale horn; variably conspicuous malar stripe of dark neutral gray. Mantle background light neutral gray completely barred with dark neutral gray. Breast and belly white to pale horn color (breast occasionally salmon) moderately barred (anteriorly) and spotted (posteriorly) with dark neutral gray. Tail pale horn color to light neutral gray heavily to moderately barred with blackish neutral gray, sometimes surrounding pale spots (similar to Saker Falcon). Primaries white to pale horn color with irregular sepia bars on inner webs, and sepia with irregular white to pale horn color spots on outer webs; secondaries white to light neutral gray incompletely barred with a dilution of sepia; underwing coverts and axillaries white to pale horn color barred with blackish neutral gray.

Dark variants overall Van Dyke brown, except breast and belly background varying from pale neutral gray (86) to pale pinkish buff (121D) heavily streaked (anteriorly) and barred (posteriorly) with Van Dyke brown; tail neutral gray strongly barred with Van Dyke brown, darker color often mottling lighter color, barring faint in darkest individuals; primaries and secondaries pale horn mostly obscured with heavy irregular sepia barring or heavy mottling; underwing coverts and axillaries heavily barred with Van Dyke brown, leaving only small spots or barring of white background.

Bare Parts

Bill.

Yellow (white variants) to bluish horn (gray/intermediate and dark variants) with darker tip in first-cycle (sometimes completely dark in juveniles of dark variants) and paler (sometimes with almost translucent tip) in adult male. Adult dark variant bill variable, ranging from blue horn with blackish tip to blackish fading to yellowish horn at base.

Cere and gape greenish bluish gray to greenish (first-cycle) to yellow (adults). Bill and cere colors can be slow to develop, duller in second-cycle than in older birds,

and also tend to be brighter in males than in females. Hatchlings with bill paler and cere and gape pinkish to yellowish.

Iris.

Dark brown in all ages and variants.

Legs and Feet.

Pinkish (hatchlings) to greenish blue-gray (first-cycle) to yellow (adults). Leg color may be intermediate during second cycle and, in adults, averages brighter yellow in males than females. Talons pale horn (white variants) to dark horn or black (dark variants).

MEASUREMENTS

Mass

Largest species in genus *Falco*, males from 800 to 1400 g, females 1000 to 2100 g (lower values probably from individuals in poor physical condition, Cade et al. 1998a). One captive male with West Nile Virus dropped from normal weight of 1150-1200 g to 750 g and survived to regain normal weight and activity (TJC). Mass of normally functioning individuals can vary by 250-500 g depending on sex and nutritional state (Cade et al. 1998a). Moderate reversed sexual size dimorphism: In series of 5 geographical samples male averages for mass ranged from 64.3% to 74.0% of female averages (Brown and Amadon 1968, Cramp and Simmons 1980, Clum and Cade 1994, Cade et al. 1998a, Potapov and Sale 2005). No geographic trends noted in sexual size dimorphism. Slight geographic differences in overall size: Largest birds occur in Iceland and Greenland, smallest in North America and Scandinavia. Apparent trend towards increase in size from west to east in Eurasia (Dementiev 1960, Palmer 1988, Clum and Cade 1994, Cade et al. 1998a, Potapov and Sale 2005). No seasonal change in body mass documented, but data are few.

Linear

See Table 1.2. Linear measurements show slight geographic variation and parallel differences in body mass and findings of significant genetic difference between island (Greenland and Iceland) and continental (Europe and North America) populations (Johnson et al. 2007). As examples, wing length of museum skins measured flat for worldwide sample of 243 males was 368.2 mm ± 12.64 mm (SD), and for 362 females, 403.9 mm ± 12.44 mm (SD) (Potapov and Sale 2005). For Iceland, male wings of 4 live specimens measured flat averaged 373 mm ± 8.0 mm and for 23 females, 419 mm ± 5.0 mm (Cade et al. 1998a); for West Greenland, 4 live males measured flat averaged 378.5 mm (range 370-386 mm), and 9 females, 414.3 mm (range 404-420) (Mattox 1970). In two estimates for North America, 20 male specimens measured flat averaged 367 mm (range 340-390 mm), and 38 females, 393 mm (range 345-410 mm) (see Table 1.2); 42 male specimens measured flat averaged 364 mm (range 340-378 mm) and 63 females, 400.5 mm (range 368-423 mm (Todd and Friedmann 1947)). See other summaries in Potapov and Sale (2005).

Note: Interpretation of these small differences is often confounded by unknown variables such as method of measurement (e.g., chord or flat wing) and whether from dried museum skin or living bird.

Linear dimensions show moderate reversed sexual size dimorphism (RSD) by comparison with other falcons and accipiters. Using Storer's (1966) Dimorphism index (mean of females – mean of males ÷ mean of males ÷ 2 + mean of females ÷ 2 X 100) for wing length: mean Gyrfalcon 9.5 (n=4), Merlin 9.6 (n=5), Saker 9.7 (n=1), Lanner 11.9 (n=1), Aplomado Falcon 11.9 (n=2), Peregrine 12.9 (n=5), Prairie Falcon 13.5 (n=3), Bat Falcon 15.1 (n=2), Goshawk 9.9 (n=3), European Sparrowhawk 16.7 (n=1); Sharp-shinned Hawk 17.1 (n=2) (data from Friedmann 1950, Storer 1966, Snyder and Wiley 1976, Cramp and Simmons 1980). Among other measurements of Gyrfalcon, the RSD index is least for length of the tarsometatarsus (4.8, 5.9) and middle toe (8.6, 8.9).

The lesser overall RSD of the Gyrfalcon compared to the Peregrine and other bird-feeding specialists, and particularly the small sex difference in size of "tarsus" and toes, may be related to the fact that both sexes feed predominantly on ptarmigan (*Lagopus* spp.) weighing around 500-650 g, each sex having converged toward the body and foot size best adapted to that size of prey (TJC).

PRIORITIES FOR FUTURE RESEARCH

Although the Gyrfalcon is an impressive species, much sought after by birders, biologists, and falconers, its relative inaccessibility has left many aspects of its biology unstudied. With a few notable exceptions, samples sizes of Gyrfalcon studies have been very small, often fewer than 10 nests or individuals. This makes generalizations difficult at best and highlights the need for larger, collaborative studies.

The origin of and factors maintaining the extreme variation in plumage color of the species, along with regional differences in proportion of variants, are still largely unknown. These issues are beginning to be addressed using molecular techniques but representative samples from its circumpolar distribution are needed. Investigations of the progression of plumages (if any) between Juvenile and Definitive is also needed. Information on survival rates, longevity, the timing and direction of dispersal, nest site fidelity, and the degree and nature of adult migration is severely lacking. Almost no information exists on the presence, size, or ecology of the non-breeding population. Gyrfalcon eggs, chicks, and adults are all remarkably tolerant of temperature extremes, so investigations into the physiological ecology of this species would be of interest, particularly in regard to food availability in winter.

Another area of continuing controversy is the nature and cause of annual fluctuations in breeding populations of Gyrfalcons and what factors cause populations to fluctuate (or not) differently. This continues to be a problematic area for research because of the long-term, large scale commitment of resources necessary to address the issue properly.

Another more basic problem is achieving accurate population estimates. Although a number of researchers expend considerable effort to monitor populations, all agree that a large portion of potential Gyrfalcon habitat remains unsurveyed. Current survey techniques rarely incorporate measures of detectability, forcing monitoring programs to rely on indices of population change instead of actual estimates. Efforts should be made to create common survey methodologies that include measures of detectability and that allow for international comparisons to monitor for population change.

Last, as the Gyrfalcon faces its perhaps most significant threat, global warming, we need long-term, international collaborative investigations into the effects of warming on the species, its population status, and how it adapts or fails to adapt to its changing Arctic environment.

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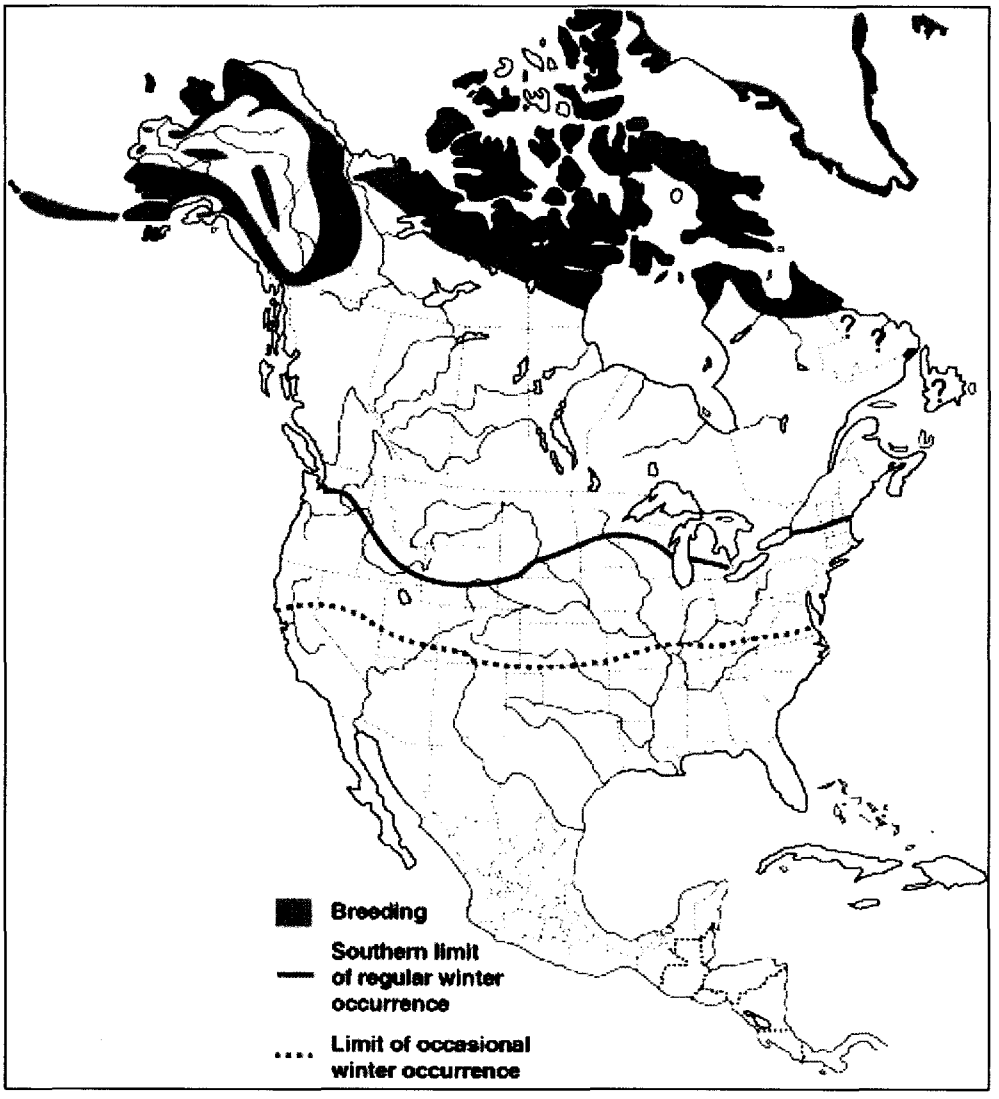

Figure 1.1. Gyrfalcon Distribution. Breeding and wintering distribution of Gyrfalcons in North America.

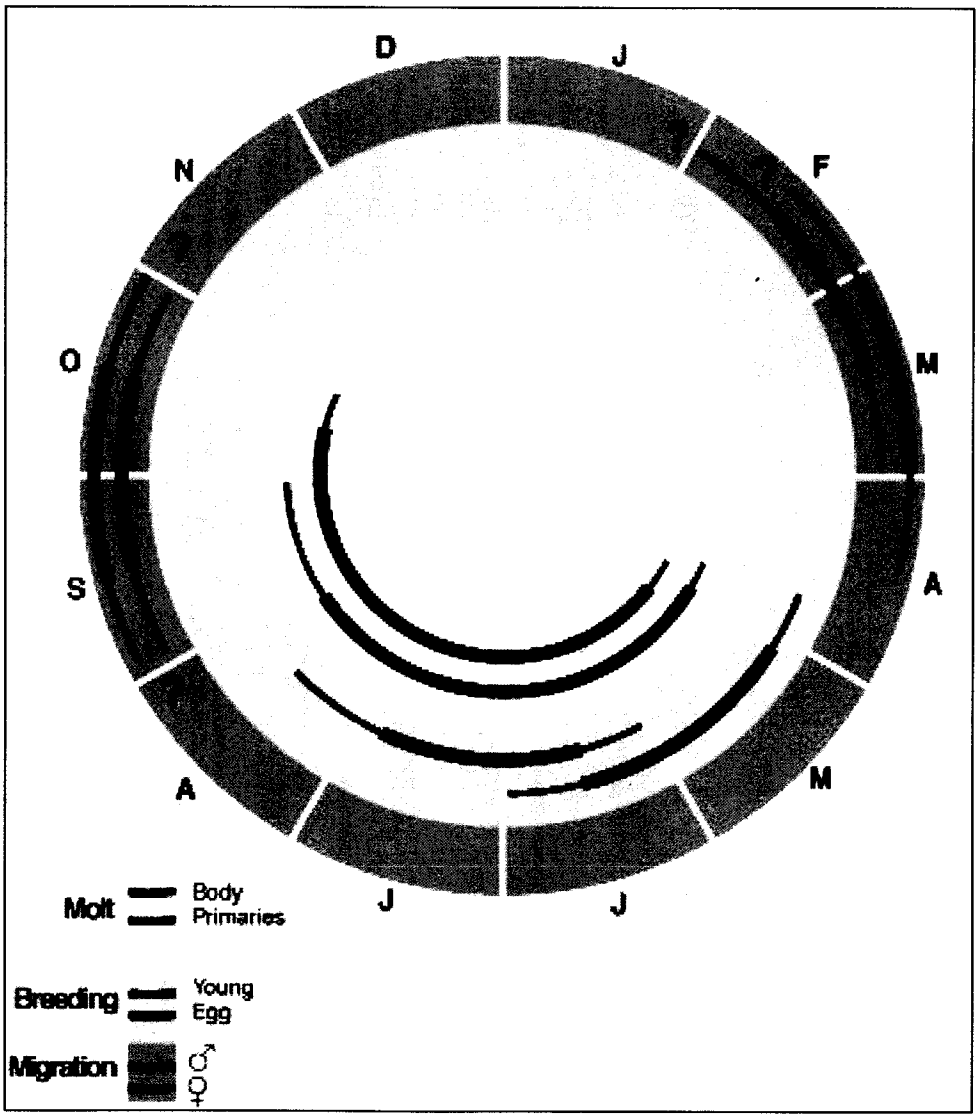

Figure 1.2. Annual Cycles of the Gyrfalcon. Thicker lines represent peak activity, thinner lines represent off-peak activity.

Table 1.1 Geographical Variation in Gyrfalcon Diet[1].

	Alaska Range[2]	Ellesmere Island[3]	Hooper Bay[4]	Yukon Territory[5]	Seward Peninsul
Latitude	64° N	78° N	62° N	69° N	65° N
Elevation	>1,000 m	<100 m	<100 m	<600 m	<450 m
Distance to Coast	>300 km	within 10 km	within 5 km	within 100 km	within 75 km
Birds					
Ptarmigan	45 (56)	2 (3)	24 (39)	61 (79)	59 (72)
Waterfowl	1 (1)	<1 (<1)	31 (47)	-	14 (12)
Shorebirds[10]	1 (<1)	27 (9)	29 (13)	4 (1)	5 (2)
Passerines	8 (<1)	6 (1)	16 (1)	10 (1)	6 (<1)
Raptors	-	-	-	-	1 (1)
Total Birds	55 (57)	35 (13)	100 (100)	75 (81)	85 (87)
Mammals					
Ground squirrels[11]	38 (42)	<1 (<1)	-	15 (18)	12 (13)
Lagomorphs[12]	<1 (1)	23 (82)	-	-	-
Microtine rodents	7 (<1)	42 (5)	-	10 (1)	3 (<1)
Total Mammals	45 (43)	65 (87)	0	25 (19)	15 (13)

[1]Values represent frequency in diet estimated from pellets and prey remains; numbers in parentheses are pe
between passerines and small mammals.

[2]Bente 1981 , n = 2 nests, 2 yrs and 323 remains; percent by mass calculated by NJC, frequencies recalcul

[3]Muir and Bird 1984, n = 1 nest, 1 yr and 732 remains.

[4]White and Springer 1965 , n = 1 nest, 1 yr and 38 remains; percent by mass calculated by NJC.

[5]Platt 1977 , n = 1 nest, 2 yrs and 105 remains; percent by mass calculated by NJC.

[6]Roseneau 1972 , n = 10–16 nests, 3 yrs and 1,483 remains.

[7]Poole and Boag 1988 , n = 0–4 nests, with concentrated collection at 3–4 sites, 3 yrs and 1,003 remains.

[8]White and Cade 1971 , n = 3 yrs and 618 remains; percent by mass calculated by NJC.

[9]Booms and Fuller 2003b, n=22 nests, 2 years, 1035 prey items.

[10]Includes Larids.

[11]Includes Mustelids.

[12]Includes marmots.

orthwest Territories[7]	Colville River[8]	Central West Greenland[9]
68° N	69° N	67° N
<375 m	<150 m	<800 m
within 20 km	within 150 km	within 150 km
65 (73)	91 (95)	78 (75)
1 (2)	2 (2)	5 (8)
1 (<1)	1 (<1)	0
11 (1)	<1 (<1)	2 (1)
-	2 (2)	0
78 (76)	96 (99)	88 (82)
14 (14)	1 (1)	0
3 (10)	-	11 (18)
5 (<1)	3 (<1)	0
22 (24)	4 (1)	12 (18)

by mass. Unidentified species are divided equally

without supplementary food.

Table 1.2. Morphological Measurements of Adult Gyrfalcons[1].

	Mean (SD, range)	n	P[2]
Culmen (mm)			
Male	22.6 (1.3, 20.2–25.3)	8	<0.001
Female	25.3 (1.3, 22.9–28.1)	37	
Wing (cm)[3]			
Male	36.7 (1.1, 34.5–39.0)	20	<0.001
Female	39.3 (1.4, 34.5–41.0)	40	
Tail (cm)			
Male	21.3 (1.6, 19.5–24.5)	11	<0.05
Female	22.7 (2.1, 21.0–29.0)	38	
Tarsus (mm)			
Male	60.9 (4.6, 52.1–68.7)	21	NS
Female	62.3 (4.3, 48.9–74.6)	38	
Toe (mm)[4]			
Male	55.3 (2.8, 51.0–61.3)	13	<0.001
Female	61.0 (3.5, 51.9–66.1)	22	

[1]North American study skins from the American Museum of Natural History, Field Museum of Natural History, and Museum of Comparative Zoology, measured by NJC.

[2]Sex differences determined by Pooled (equal variance) T-test.

[3]Wing chord measured closed and flattened.

[4]Middle toe measured with talon.

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Chapter 2. Gyrfalcon Nest Distribution in Alaska based on a Predictive GIS Model.[1]

ABSTRACT

The gyrfalcon (*Falco rusticolus*) is an uncommon, little studied circumpolar Arctic bird that faces conservation concerns. We used 455 historical nest locations, 12 environmental abiotic predictor layers, Geographic Information System (ArcGIS), and TreeNet modeling software to create a spatially explicit model predicting gyrfalcon breeding distribution and population size across Alaska. The model predicted that 75% of the state had a relative Gyrfalcon nest occurrence index value of <20% (where essentially no nests are expected to occur) and 7% of the state had a value of >60%. Areas of high predicted occurrence were in northern and western Alaska. The most important predictor variable was soil type, followed by sub-surface geology and vegetation type. Nine environmental factors were useful in predicting nest occurrence, indicating complex multivariate habitat relationships exist. We estimated the breeding gyrfalcon population in Alaska is 546 ± 180 pairs. The model was 67% accurate at predicting nest occurrence with an area under the curve (AUC) score of 0.76 when assessed with independent data; this is a good result when considering its application to the entire state of Alaska. Prediction accuracy estimates were as high as 97% using 10-fold cross validation of the training data. The model helps guide science-based management efforts in times of increasing and global pressures for this species and Arctic landscapes.

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[1] Booms, T.L., F. Huettmann, and P.F. Schempf. 2010. Gyrfalcon nest distribution in Alaska based on a predictive GIS model. Polar Biology: 33:337-346.

INTRODUCTION

Species distribution is essential knowledge for conservation biology (Araujo and Guisan 2006). The distribution of a species is informed by its ecological niche, defined by Hutchinson (1957) as the set of biotic and abiotic conditions in which a species is able to persist and maintain stable population sizes. The ecological niche is both the fundamental niche (defined by abiotic factors) and the realized niche (defined by abiotic and biotic factors). Learning what variables contribute to defining the boundaries of either of these types of niches informs our understanding of the species' ecology, can be used to predict the distribution of the species, and is often relevant for specific management actions (Peterson 2001).

Understanding where species occur temporally and spatially across large geographic areas is important to conserving, monitoring, and managing species effectively (Wu and Smeins 2000). However, detailed species distribution data spanning large areas are rarely available, especially for remote Arctic areas. Extrapolating beyond areas of known presence, using predictive modeling, helps to estimate distribution, particularly for rare or endangered species in remote areas (Peterson 2001, Pearce and Boyce 2006). It is a convenient and cost-efficient approach making use of data collected during previous decades. Such predictive models are valuable for guiding conservation actions and planning (Heglund 2002). For example, a model that evaluated habitat suitability for the endangered timber wolf (*Canis lupis*) was useful in the recovery of the species because it gave managers a realistic idea of future population size and distribution (Mladenoff et al. 1995, 1999).

The gyrfalcon occurs at low densities across the circumpolar Arctic (Cade 1982) where it breeds above 55° N. It is an important apex predator to the Arctic ecosystem that feeds on ptarmigan (*Lagopus* spp.) (Booms et al. 2008). It relies on cliff and cliff-like structures for laying its eggs on rock ledges or in stick nests built by other bird species (Palmer 1988). Our understanding of the variables that influence gyrfalcon distribution is limited and based on findings from small geographic areas. The global

breeding population estimate is roughly 8 000 – 11 000 pairs (Potapov and Sale 2005) and though the gyrfalcon is not listed as endangered or threatened in North America, it is a C.I.T.E.S. Appendix 1 species. Current best estimates of its breeding distribution in Alaska are based on expert opinion and largely extrapolated from a few areas that have been well surveyed (Swem et al. 1994). However, a large portion of the state has not been surveyed, and the state's full potential for gyrfalcon nesting habitat is largely unknown (Swem et al. 1994). Data from the few areas that are regularly surveyed in Alaska have not been combined to address statewide conservation issues for a synthesis or to investigate ecological questions beyond local scales.

Though gyrfalcons inhabit remote areas, the species will likely face serious conservation threats from resource development issues and global warming through changes in vegetation and prey species (Booms et al. 2008). Arctic portions of Alaska are believed to contain the second largest deposit of oil and oil-equivalent natural gas in the world (U.S. Geological Survey 2008), and development activities could potentially affect Alaska's gyrfalcon population. The potential for wind turbine developments along coastal Alaska is another threat to the species. Coastal areas that are classified as having "outstanding" or "superb" potential for wind development (U.S. Department of Energy 2008) are also important to gyrfalcons (Britten et al. 1995). Because wind turbines are known to kill large numbers of birds (Johnson et al. 2001) including falcons (Smallwood and Thelander 2004), and have the potential to reduce populations of resident raptors (Hunt et al. 1999), wind turbines could impact Alaska's gyrfalcon population. Therefore, identifying potential hotspots for breeding (and potential conflict with development) is important to conserving the species. Gyrfalcons will be impacted by global warming because Arctic habitats are predicted to be significantly affected (Booms et al. 2008). In Alaska, the mean annual temperature has warmed by as much as 2.2°C in the past 50 years (Stafford et al. 2000) and such warming has been associated with deleterious changes in bird nesting phenology (Crick 2004). Shrub growth is increasing in Arctic Alaska (Tape et al. 2006) and drying is expected, changing the structure of the open tundra used by gyrfalcons for hunting. Increased shrubs may provide additional cover for

ptarmigan, reduce gyrfalcon foraging efficiency, and could impact gyrfalcon population growth and distribution.

We compiled gyrfalcon nest locations in Alaska and created a model to predict breeding locations for gyrfalcons (its fundamental niche) based on factors measured at historical nest sites. Guided by the resulting model, we then collected independent, spatially explicit evaluation data to assess model accuracy. To our knowledge, this is the first predictive, spatial model of breeding gyrfalcons anywhere and a step towards developing a global conservation effort to assess uncertainties. We also present an innovative technique to model sensitive data (nest locations) without having to obtain the actual locations. Our specific research goals were: (1) estimate the breeding distribution and population size of gyrfalcons in Alaska, (2) determine the relative importance of a suite of environmental variables that explain the breeding distribution, and (3) assess the accuracy and utility of the model. The results help inform us about the factors influencing gyrfalcon nesting and guide future sampling, surveying, and conservation efforts across the state.

METHODS

Environmental Layers

We chose 12 environmental variables to develop the model based on availability and our knowledge of gyrfalcon ecology and published literature (Booms et al. 2008). All data layers were publicly available and had statewide coverage (Table 2.1). We re-projected layers into Clark 1866 Albers (in meters) and merged them for a consistent statewide coverage. All geographic information system (GIS) operations were conducted in ArcMap 9.2. and 9.3 (Environmental Systems Research Institute 2008). Slope and aspect layers were derived in ArcMap from an official state-wide digital elevation model. We calculated the distance to fresh water, coastline, and human structures using the Euclidean distance tool in ArcMap 9.2. Aspect data were categorized into four directional groups (N = 316-45°, E =46-135°, S = 136-225°, W = 226-315°, and flat) and used as a categorical variable. We used average April temperature and precipitation

because we expected breeding gyrfalcons would be most influenced by these parameters in April during territory establishment and early incubation.

Training Data

We obtained 414 gyrfalcon nest locations spanning all types of gyrfalcon nesting habitats in Alaska between 1972 and 2007 from collaborators to use as training data (Figure 2.1). We did not differentiate between successful nests (potentially higher quality sites) and unsuccessful nests (lower quality sites). Nests were found during a 36-year period including some from the 1960s or earlier (Cade 1960), making the dataset one of the largest and longest term collections of raptor nest locations used for predictive modeling in Alaska, and likely elsewhere. Nest locations were converted to WGS-84 datum, re-projected into Clarke 1866 Albers, and imported as a shapefile layer into GIS. Gyrfalcon nest locations in Denali National Park were provided to us as the extracted environmental data (see methods below). A total of 455 nests were used in our model.

We created 10,000 random points across Alaska using the freely available Hawth's Tools in ArcGis (Beyer 2008). We used these points as a measure of available habitats against which we compared the 455 nest locations (Manly et al. 2002, Engler et al. 2004). The ratio of 455 presence vs. 10 000 pseudo-absence points is commonly used in the modeling literature (Craig and Huettmann 2008) and the uneven ratio is corrected by using balanced weight settings in TreeNet.

Modeling Approach

We used presence-available modeling to predict nest occurrence following design II in Manly et al. (2002) (Pearce and Boyce 2006). We extracted information from environmental layers at historical nest sites and random points in ArcMap 9.3 using Hawth's Tools. We subjected these data to stochastic gradient boosting algorithms using program TreeNet 2.0 (Salford 2002). Stochastic gradient boosting is part of regression tree analysis (Friedman 2002) that creates binary trees by recursively partitioning data

into two data sets based on predictor variables while trying to minimize variation within each dataset. Subsequent trees are constructed for the prediction of the residuals from the previous trees and results are computed from the entire group of trees (Friedman 2002).

We constructed our model in TreeNet using binary logistic regression and the balanced class weights option to account for unequal sample sizes of presence and available points. Otherwise, we used default setting in TreeNet and allowed it to optimize the number of trees in the model. Because the optimal number of trees was less than 150, there was no need to build additional trees to further optimize the model (Salford 2002).

For prediction to data, we created a point lattice grid of 18,000 regularly spaced points across Alaska (approximately 7 x 7 km spacing), and extracted information from the 12 environmental layers (Table 2.1) described above for each point. We then used the optimized model to predict nest presence at each of the 18 000 points based on the extracted environmental data at each point. Predicted presence was scaled from 0-100% and interpreted as the relative index of occurrence (Keating and Cherry 2004, Araujo and Williams 2000). We imported the dataset of spatially referenced predictions into GIS as a raster file and interpolated between the regular points using inverse distance weighting (IDW) to obtain a smoothed predictive map of gyrfalcon nest distribution.

To estimate the state's breeding population, we assigned density estimates to each predicted category (Nielsen et al. 2008, Onyeahialam et al. 2005) from the range of published nesting densities found in Alaska (one nest per 200-1000 km^2) (Swem et al. 1994) (Table 2.2). Based on our experience with the species, we assumed no gyrfalcons bred in areas with predicted occurrence levels $\leq 40\%$. We multiplied the total area of Alaska covered by each prediction category by the corresponding density estimate and summed the totals to estimate the state population, similar to Boyce and McDonald (1999) (Table 2.2). We multiplied the final estimate by the model's accuracy, as determined by independent survey data, to provide a measure of error around the estimate. The total area of Alaska used in our analysis is 1 481 000 km^2 (U.S. Census Bureau 2004).

Model Evaluation

We evaluated the model thoroughly using internal training data as well as two types of independent data: 1) the number of potential nest cliffs in plots and 2) the presence or absence of an occupied gyrfalcon nest in plots. We defined a potential nest cliff as any rock structure with a vertical rock face $\geq$ 4 m, based on published descriptions of gyrfalcon nest cliffs (Booms et al. 2008) and 8 years of field experience working with the species. We assumed a priori that the second measure of accuracy in the independent data (occupied nests) would be biased low because it was influenced by biotic variables that we did not attempt to model. This sets up a mismatch between modeling the fundamental niche and measuring model accuracy with the realized niche. However, we included this measure of accuracy for completeness because it would be biologically informative to learn how well the model predicted both occupied and potential nest sites.

Evaluation with Internal Training Data

We used the aspatial 10-fold cross validation procedure in TreeNet which divided the original training data into 10 groups and used 9 of the groups as training data. The remaining group was used as testing data. This was done ten times and a different group of data was withheld for testing each time. Testing results were then averaged across the ten iterations and the area under the curve (AUC) estimate in the receiver operating curve (ROC) plot was taken directly from TreeNet to assess prediction accuracy. We considered AUC scores <0.7 indicated low model accuracy, 0.7-0.9 moderate accuracy, and >0.9 high accuracy (Swets 1988).

Independent Spatial Data

We evaluated the model with spatially explicit independent data collected after the model was built and believe this approach provides the most reliable assessment of accuracy.

Many studies fail to test model accuracy spatially and in the field using additional, independent data (Heglund 2002) and instead only evaluate model accuracy by re-sampling or partitioning training data (Manel et al. 2001). Data partitioning methods such as k-fold partitioning reduce the sample size of training data and though they are an acceptable method of evaluation, they are less effective and meaningful than using independent and truly spatial data (Verbyla and Litaitis 1989, Fielding and Bell 1997, Fielding 2002).

We ground-truthed the model by conducting landscape-scale aerial surveys in model-predicted areas to learn if predictions correctly classified gyrfalcon nest occurrence in survey plots in May and June 2008. We selected three study areas for which the model predicted high gyrfalcon nest occurrence (> 80%) but for which no training data were present: the Lisburne Peninsula in northwest Alaska, parts of the Arctic National Wildlife Refuge in northeast Alaska, and parts of the Togiak National Wildlife Refuge in southwest Alaska (Fig. 2.2).

We placed circular, 50-km^2 plots (4 km radius) in each study area within each of three predicted occurrence categories: "high" (predicted >80% occurrence, n=5), "moderate" (60-40%, n=6), and "low" (<20%, n=7). Survey plots were paired and located within 10 km of each other within each prediction category to reduce travel time between plots (Figure 2.2). We subjectively located paired plots within 160 km of a runway to provide plane access and refueling options. No other information was used to determine plot location, and we had no prior knowledge of gyrfalcon occurrence in the study areas. We attempted to survey 10 plots in each predicted occurrence category across the state (30 total), but poor weather allowed only 18 plots to be surveyed. Additionally, we had planned to conduct repeat surveys on the 30 plots to estimate detectability and correct for imperfect detection, but poor weather prevented this.

We chose the 4-km radius plots because that was the approximate pixel size of the predictive layer and because the size allowed us to survey two plots per flight based on plane fuel capacity and consumption. Our ArcGIS plot and survey maps were transferred to Google Earth to be publicly and easily available to our survey pilots. Each plot was

surveyed by TB and a pilot using a two-seat Piper Super Cub or Aviat Husky fixed-wing plane for 40-120 minutes, depending on the geographic complexity of the plot. The plane was flown as low and slowly as was safely possible given conditions, typically 60 m above the ground (range 30-200 m) at 110-130 km/h. We recorded the number of occupied gyrfalcon nests (a nest with eggs, young, or territorial adults) and the number of potential nest cliffs found in each plot.

Gyrfalcons may not breed every year even in good quality habitat because of natural fluctuations in prey, weather conditions, and other stochastic variables (Nielsen and Cade 1990a). Therefore, it was possible that a plot could have been occupied by breeding gyrfalcons in some years but not in the year we surveyed it. Additionally, detecting raptors during aerial surveys can be difficult (Andersen 2007, TLB unpubl. data), and it is possible that we failed to detect a few occupied sites during our surveys. Hence, collecting information on the presence of both occupied and potential nest sites on plots provided us with a more comprehensive understanding of model accuracy in terms of fundamental and realized niches, imperfect survey detectability, and the underlying biological mechanisms.

For evaluation purposes, we considered a plot as occupied (true positive finding) if it contained an occupied gyrfalcon nest or had > 5 potential nest cliffs on the plot. We chose five cliffs as a cut-off value after completing the surveys because that was the minimum number of cliffs found on a plot in which an occupied gyrfalcon nest was also detected. We assessed model accuracy by comparing the predicted gyrfalcon nest occurrence value of each plot (high = 0.9, moderate = 0.5, low = 0.1) to the occupancy status of the plot determined by aerial surveys. We then created a confusion matrix for each dataset using counts of true positive, false positive, true negative, and false negative results when comparing predicted versus observed data. We used receiver operating curve (ROC) graphs and area under the curve (AUC) scores to interpret model accuracy (Fielding and Bell 1997). Calculations were performed in publicly available online program ROC Plot (Schroeder 2004) for the independent survey data.

General Methods

Several logical biases deserve attention. First, presence data were obtained opportunistically and may not capture the full spectrum of variation in gyrfalcon nesting preferences or its ecological niche. This could introduce bias if presence data were not representative of most of the natural variation and gradients in nesting areas. However, presence data came from all regions of Alaska where gyrfalcons are documented to bred (Figure 2.1). Second, it is possible that gyrfalcon nesting distribution may have changed over the course of the 36+ year dataset such that the resulting model may not apply to the current breeding population. A large-scale shift in nesting occurrence over this period of time is unlikely because gyrfalcons are relatively long-lived birds (Nielsen and Cade 1990a) and likely have high nest site fidelity (Nielsen 1991) with many nesting areas used repeatedly by generations of gyrfalcons. For example, some historical gyrfalcon nest sites in Greenland have been occupied by gyrfalcons and other raptors for the last 2,500 years (K. Burnham unpubl. data). Third, was the scale (extent and pixel size; Wu and Hobbs 2002, Huettmann and Diamond 2006, Guisan et al. 2007) appropriate for the work? We selected Alaska as our extent because it was the appropriate political management unit for implementing conservation actions and it is large enough to include much of the inherent variation in nesting occurrence for the species, making results informative about the species as a whole and on a global level. We assume the entire state was available to gyrfalcons because they move across the state (Britten et al. 1995) and into Canada and the lower 48 United States (Sanchez 1993). Pixel size was determined by environmental layers publicly available with statewide coverage; most were 1 km or less and therefore adequate for modeling occupied nest locations (which were typically separated by 10 - 100 km).

RESULTS

Nine of 12 environmental variables predicted gyrfalcon nest occurrence (Table 2.1). The most important predictor variable was soil type, followed by sub-surface geology and vegetation type. Gyrfalcon nests were most commonly associated with pergelic

cryaquepts, soils that were typically wet, frozen, and had high organic content and had gravelly, steep slopes (Rieger et al. 1979) (Table 2.3). The most common subsurface geology associated with nest sites were Quaternary mafic volcanic rock such as basalt and Ordovician limestone and shale. Nests were most associated with dwarf shrub tundra, alpine tundra and barrens, and ocean coast vegetation types (Table 2.3).

The optimized TreeNet model contained 48 statistical trees and predicted gyrfalcon nesting occurrence (Figure 2.3). Approximately 75% of the state was predicted to have an index of relative occurrence < 20%; 7% of the state was predicted to have an index of >60% (Table 2.2). Areas of high predicted occurrence (>80%) were patchy and widely dispersed, located in southwest, west, northwest, and northern Alaska. They included well-known breeding areas on the Seward Peninsula and in parts of the Brooks Mountain range and northern foothills. Areas of high predicted occurrence not well known as gyrfalcon breeding areas included parts of the Togiak National Wildlife Refuge in southwest Alaska, the Lisburne Peninsula in northwest Alaska (though see White and Boyce 1977), and parts of the Brooks Mountain range within the Arctic National Wildlife Refuge in northeast Alaska. These areas varied from 35-80 km in width. Using the range of published nesting densities (Swem et al. 1994), the area of each predicted occurrence category, and model accuracy as a measure of error, we estimated approximately 546 ± 180 breeding pairs (using our model accuracy estimate (67%) from evaluation plots as a measure of error) occur in the state in any given year (Table 2.2).

Using 10-fold cross validation on the training data, the optimized model was 97% and 93% accurate in aspatial terms and when assigning presence and absence, respectively. The area under the curve (AUC) was 0.96, indicating very high prediction accuracy of the data used. The model's accuracy in predicting potential nest cliffs in the independent and spatial evaluation data was 67% and had an AUC score of 0.76. This indicated the model was moderately accurate and useful when predicting potential nest cliffs in the real world. The model was 36% accurate for predicting occupied gyrfalcon nests in the evaluation data with an AUC score of 0.38, indicating the model performed

worse than if presence/absence were assigned randomly when tested with data from the realized niche.

DISCUSSION

It is useful to think of the variable with the lowest predictive value (aspect) as defining the outer boundary of the species' fundamental niche in multidimensional space. Each subsequent predictor variable (in this case, digital elevation, April temperature, distance to coast, etc.) sequentially shrinks the niche in multidimensional space as each variable increases in its predictive ability, until all abiotic factors have been considered. The resulting space is the fundamental niche and is most restricted by the variables with the most predictive influence: vegetation type, subsurface geology, and soil type for gyrfalcons. The fundamental niche could be further sequentially refined using biotic variables that influence the species' ability to persist such as prey, competing species, and individual fitness. The core of this multidimensional space is the species' realized niche in space and time and its description is the ultimate conservation biology goal. Here we contribute to this effort by describing the fundamental niche because of its relative simplicity compared to the complex realized niche.

The importance of soil type, sub-surface geology, and vegetation type in the model likely reflects their relative importance in the species' ecology. It is important to note, however, that the variables we found to be relatively unimportant in this study may play an important role in falcon ecology at other scales, locations, or systems. For example, Urios and Martinez-Abrain (2006) found that elevation, aspect, slope, and distance to human developments were important in describing nest site preferences of Eleonora's Falcons (*Falco eleonorae*) on a Mediterranean island but they were of relatively low importance in this study.

Gyrfalcon nests were commonly found on Pergelic Cryaquepts soils that support tundra and dwarf shrub vegetation on which the gyrfalcon's prey (ptarmigan) depend. Sub-surface geology ranked high as a predictor variable because the underlying geology greatly determined cliff occurrence on the landscape. Gyrfalcon nests are associated with

volcanic rocks (basalt) and sedimentary rocks (limestone and shale), which probably produce more cliffs than other types (alluvial deposits). The predominant vegetation types associated with nests match our current understanding of gyrfalcons as an obligate tundra breeder. They provide gyrfalcons ptarmigan and the open environments needed to capture them. Nests were also associated with ocean coastline vegetation, which may seem surprising. However, we suspect gyrfalcons are selecting such areas in some regions because they provide direct access to seabirds, a common alternative food source (Nielsen and Cade 1990b). This finding is particularly interesting because coastal habitats are also valuable to non-breeding gyrfalcons (Britten et al. 1995) and have high potential for wind turbine developments that may cause conservation conflicts (U.S. Department of Energy 2008).

Our Alaska gyrfalcon population estimate was higher than Swem et al.'s (1994) estimate of 375-635 pairs. Issues that influenced our population estimate include: 1) We subjectively assigned nesting densities to predicted occurrence categories based on published estimates and our own knowledge base with the species. Future population estimates may change if the density estimates or biological knowledge changes. 2) Our attempts to assess model accuracy with independent data are only first steps in validating the model. Clearly, increasing the number and distribution of evaluation plot surveys would improve confidence in our accuracy estimate. 3) The actual population varies by year because of stochastic events and because gyrfalcons respond numerically to fluctuating ptarmigan populations (Nielsen 1999). 4) Estimating the area that should be used for density estimate extrapolations is complex, e.g. whether lakes are to be excluded, and can affect population estimates.

Results from our accuracy assessments suggested the model was highly accurate (93-97%) when using re-sampling methods and moderately accurate (67%) when using independent data. Studies using data-mining techniques with internal accuracy assessments reported very high accuracy assessments, especially when compared to more traditional modeling techniques such general linear models (Elith et al. 2006). However, models of complex biological systems with very high prediction accuracy are unusual

and should be viewed with scrutiny because the complex nature of biological systems makes them difficult to capture and predict. Typical ecological models such as general linear models have much lower prediction accuracies because of this (Fielding 2002). Evaluating a model spatially with independent field data, as we did, provides a more realistic and accurate assessment of model accuracy and is preferred (Fielding and Bell 1997, Manel et al. 1999). Tests with independent data often reduce initial accuracy; our accuracy assessments support this finding and that predictive models need to be evaluated with independent data to assess true accuracy (Heglund 2002) and to gain credibility among managers and other decision makers.

The best measure of our model accuracy was the count of potential nest cliffs obtained from plot surveys. This measure was not influenced by complex biotic variables, was in line with our attempts to model the fundamental niche (as determined by abiotic factors), and was a true measure of model performance in the real world. The model's AUC score was 0.76 when assessed with counts of potential nest cliffs, which is considered to be moderately accurate (Swets 1988) and 'useful' (Elith and Burgman 2002). Our model should not be viewed as optimal, but rather an important first step towards refining our understanding of abiotic and biotic factors influencing gyrfalcons.

Model accuracy was low using presence/absence of occupied nests on plots, but this is unsurprising for a number of reasons. First, survey plot size was relatively small (50 km^2) compared to gyrfalcon breeding density estimates in Alaska (one pair per 170-1000 km^2) (Swem et al. 1994), and therefore under-sampling may have occurred. Low breeding densities make reliable accuracy evaluation difficult regardless of model accuracy (Henebry and Merchant 2002). Increasing plot size lowers sample size beyond desired levels because of fuel and weather limitations. Hence, plot size was a compromise between restrictive logistics and the likelihood of a plot including an occupied nest if one was present on the landscape. Second, some nests may have already failed and were unavailable to be detected during surveys. This is particularly true for the 2008 breeding season, when we observed some of the lowest occupancy and productivity rates in a long term study area in recent times in southwest Alaska (TB unpubl. data).

Third, not all occupied raptor nests are detected during aerial surveys (TB unpubl. data), and some occupied nests could have been missed (Boyce et al. 2005). Fourth, evaluating a model that attempts to predict the fundamental niche of a species with data on the realized niche is probably overly conservative. We did not include biological predictor variables that influenced breeding distribution because they were too complex to measure and were unavailable for statewide coverage. For example, stochastic ptarmigan densities influence gyrfalcon nest occupancy (Nielsen 1999) but are unavailable on a statewide or temporal basis. Therefore, the accuracy of the model using occupied nest data alone is probably not highly informative.

Wiens (2002) suggested that model accuracy is as good as the performance of the environmental layers with which it was produced. Though we used the best available layers with statewide coverage, some layers have not been rigorously ground-truthed, metadata were lacking, and their accuracy was not always known quantitatively. It is unlikely that any model using these layers can truly achieve 93-97% accuracy in the real world. Therefore, a model that captures gyrfalcon nesting ecology, distribution, and population size in one quantitative formula with an accuracy of 67% across the entire state is a significant step forward in our knowledge.

Our spatially explicit, non-linear model offers a number of advantages over non-modeling methods (Table 2.4) and linear models. First, it helps us understand complex systems in simple, transparent terms. It also provides discrete measures of relative variable importance, breeding distribution, and population size in readily interpretable formats based on objective, best available science. Second, non-linear modeling captures complex multivariate relationships not possible with linear methods (Elith et al. 2006). Criticisms of non-linear analyses such as classification and regression trees (CART) include concerns that precision is difficult to estimate, optimal trees may not be found, and results may be sensitive to small changes in data (Anderson et al. 2000, Hastie et al. 2001, Elith et al. 2006). However, stochastic gradient boosting is a refinement of the traditional regression tree analysis that addresses these concerns and improves model performance (Friedman 2002). It excels at modeling non-linear data common in

ecological studies, can handle large numbers of categorical and continuous predictor variables, performs at a faster rate than traditional techniques, and is robust to datasets that contain up to 30% faulty data in some instances (Craig and Huettmann 2008). Machine learning models such as stochastic gradient boosting produce highly accurate predictions that perform faster, are more informative, and are similar to or better than, the accuracy of traditional linear modeling approaches (Elith et al. 2006, Breiman 2001). Finding that 9 of 12 environmental variables influenced gyrfalcon distribution indicates that complex multivariate habitat and environmental relationships exist for this species and that using non-linear modeling is prudent. Third, model-based estimates enable dynamic, near-real time population estimation (instead of static ones fixed in time) and facilitates further ecological research. For example, we could include real-time data on ptarmigan distribution and population levels (if/when such become available) in modeling efforts to produce dynamic gyrfalcon population estimates. The implications for guiding fieldwork and research design are considerable including investigating spatial distribution patterns of species (fragmentation and source/sink dynamics). None of our model components are fully explored, yet deserve more attention to understand spatially explicit population dynamics.

Our model should be useful to managers addressing conservation issues in Alaska. For example, the model could be combined with existing regionalized IPCC climate models to forecast future gyrfalcon population size, distribution, and changes under varying climate scenarios (Seavy et al. 2008). Or, distribution maps could overlay maps of current and predicted locations of oil, gas, minerals, and wind resources to identify areas of potential future conflict, estimate the potential size or severity of impacts caused by a specific activity, and prioritize conservation strategies geographically.

Our modeling efforts represent a significant collating of sensitive nest location data from collaborators concerned about potential negative nest disturbance. Gyrfalcons are highly sought after by birders, and a substantial illegal harvest occurs in parts of the globe for falconry (Lobkov 2000). If made available, nest location data could negatively impact the resource. For example, we encountered resistance in Europe about sharing

nest locations; so much so that it prevented us from conducting research. Our work in Alaska is an example of the need to build partnerships, establish trust, and creatively solve problems to maintain data security while not preventing scientific learning through meta-analysis of data. Our innovative method of having a data-holder extract the relevant information from the GIS layers and provide that information to researchers instead of actual nest locations (as suggested by C. McIntyre), should be useful for others to further conservation and science when dealing with sensitive data.

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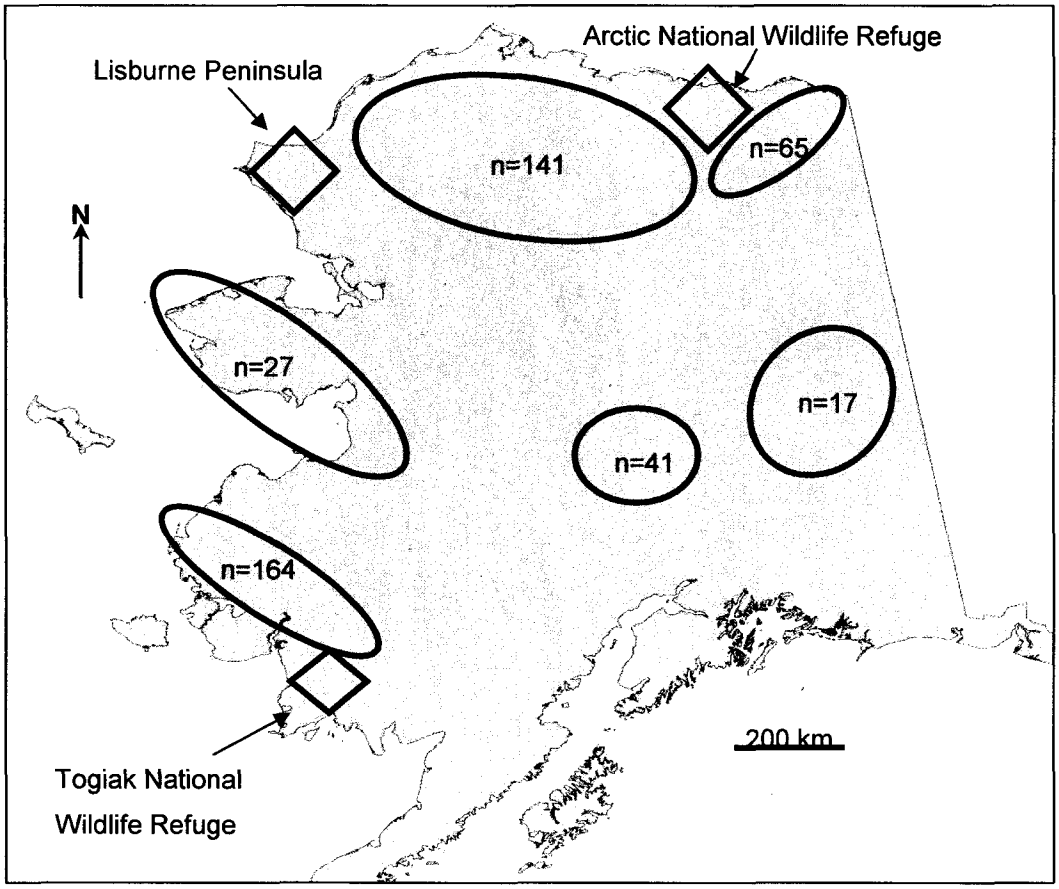

Figure 2.1. Training and Testing Data Distribution. The approximate locations of the historical gyrfalcon nests (circles) used to create the predictive model and areas used to assess model accuracy (diamonds). Study areas used to assess model accuracy included parts of the Togiak National Wildlife Refuge, Lisburne Peninsula, and Arctic National Wildlife Refuge. The number of nests (n) used to create the predictive model from each area is stated within each circle. The N arrow indicates north. Parts of southeast Alaska and the Aleutian chain are not shown because no nest data were used from these locations.

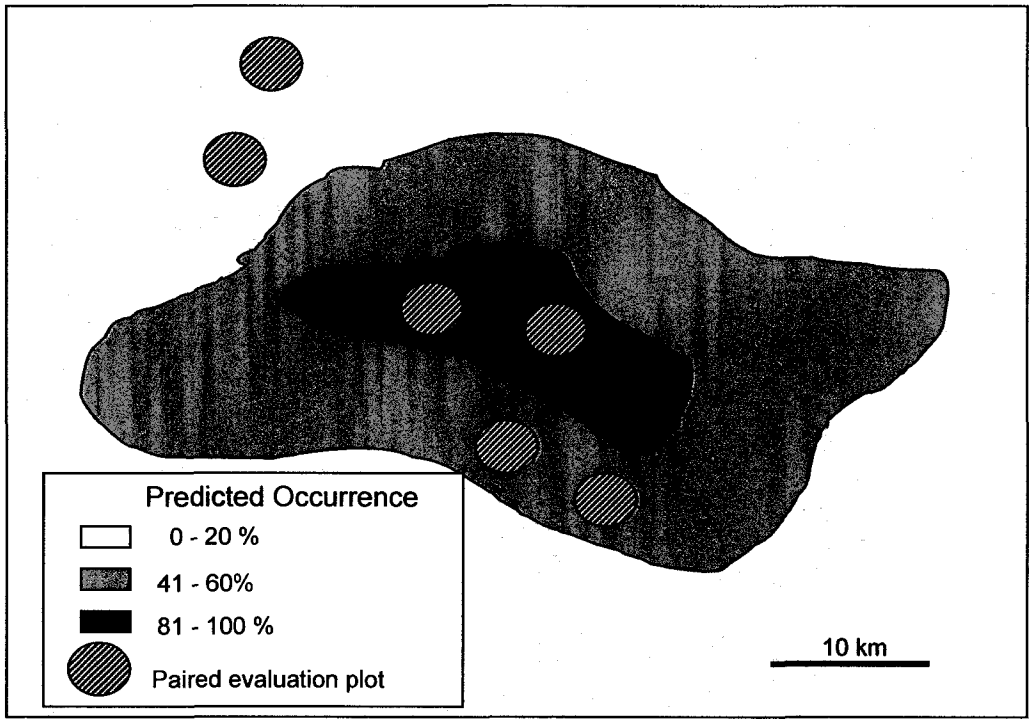

Figure 2.2. Paired Evaluation Plots. Schematic diagram of paired evaluation plots surveyed to collect independent testing data for the predictive model. Each pair of plots was placed within one of three predicted occurrence categories (0-20%, 41-60%, and 81-100%) and surveyed for gyrfalcon nest cliffs and occupied nests.

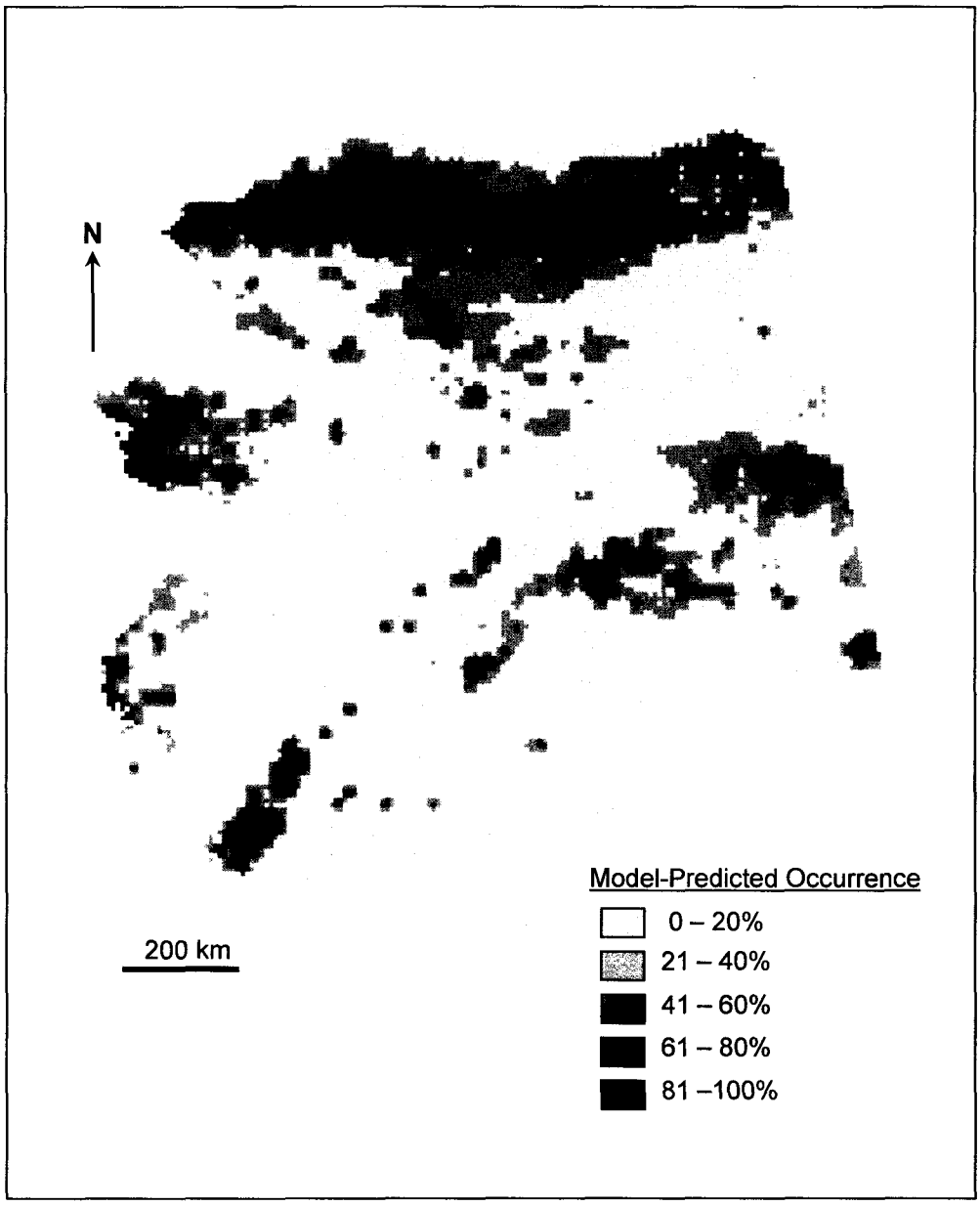

Figure 2.3. Predicted Gyrfalcon Nest Occurrence. Model-predicted map of gyrfalcon nest occurrence in Alaska (0-100% relative occurrence). Parts of southeast Alaska and the Aleutian chain are not shown, though these areas were in the lowest prediction category.

Table 2.1. GIS Layers. Environmental GIS layers used to predict gyrfalcon nest occurrence across Alaska and

Environmental Layer	Relative Importance[a]	Pixel Size	Variable Type	Number of levels	Source
Soil type	100	Polygon	Catagorical	83	Alaska Geospatial Data Clea
Sub-surface geology	58	Polygon	Catagorical	54	Alaska Geospatial Data Clea
Vegetation type	24	Polygon	Catagorical	21	Alaska Geospatial Data Clea
Surface geology	16	Polygon	Catagorical	25	Alaska Geospatial Data Clea
Slope	15	300m	Continuous	-	Alaska Geospatial Data Clea
Distance to ocean coast	10	60 km	Continuous	-	ArcGIS 9.2
Mean April temperature	8	1km	Continuous	-	Worldclim
Digital elevation model	7	300m	Continuous	-	Alaska Geospatial Data Clea
Aspect	3	300m	Catagorical	5	Alaska Geospatial Data Clea
Distance to fresh water	0	300m	Continuous	-	Global Lakes and Wetlands
Distance to human development	0	1km	Continuous	-	Center for International Earth Science
Mean April precipitation amount	0	1km	Continuous	-	Worldclim

[a] Scores taken from TreeNet.

their relative importance.		
	Citation Layer Based on	Website
inghouse	Rieger et al. 1979	http://agdc.usgs.gov/data/usgs/erosafo/soil/soil.html
inghouse	Beikman 1980	http://agdc.usgs.gov/data/usgs/geology/index.html
inghouse	Fleming 1997	http://agdc.usgs.gov/data/usgs/erosafo/veg/vegetation.html
inghouse	Karlstrom et al. 1964	http://agdc.usgs.gov/data/usgs/erosafo/surfgeol/surfgeol.html
inghouse	Derived from digital elevation model	http://agdc.usgs.gov/data/akdb/dem/dem.html
	Alaska coastline	World Coastline Extractor
	Higmans et al. 2005	www.worldclim.com
inghouse	U.S. Geological Survey 1997	http://agdc.usgs.gov/data/akdb/dem/dem.html
inghouse	Derived from digital elevation model	http://agdc.usgs.gov/data/akdb/dem/dem.html
Database	Lehner and Doll 2004	www.worldwildlife.org/science/data/item1877.html
nformation Network	Sanderson et al. 2003	www.sedac.ciesin.columbia.edu/wildareas/downloads.jsp
	Higmans et al. 2005	www.worldclim.com

Table 2.2. Population Estimate. Estimated number of breeding gyrfalcon pairs extrapolated from model-predicted nest occurrence categories and the amount of area each category covers in Alaska.

Predicted Gyrfalcon Nest Occurrence Category	Area in Alaska (km^2)	Estimated Gyrfalcon Nesting Density (nest/km^2)[a]	Total # of Estimated Nests
0-20%	1 113 000 (75%)	0	0
21-40%	141 000 (10%)	0	0
41-60%	114 000 (8%)	1/1000	114
61-80%	80 000 (5%)	1/300	267
81-100%	33 000 (2%)	1/200	165
	1 481 000		546

[a] Nest densities taken from Swem et al. (1994).

Table 2.3. Partial Dependency Scores. Partial dependancy scores of the three most influential variables predicting gyrfalcon nest occurrence in Alaska taken from response curves provided in TreeNet. Actual values are presented instead of the response curves for easier interpretation. The range of scores within each predictor variable varied from 2.6 to -0.8 for soil, 1.0 to -1.1 for subsurface geology, and 0.35 to -4.1 for vegetation. Positive partial dependency scores denote a positive association with gyrfalcon nests; negative scores indicate a negative association. Only the four highest partial dependency scores from the numerous levels within each for the three predictor variables are listed here for brevity.

Predictor Variable	Soil, Geology, or Vegetation Type	Partial Dependency Score
Soil	Pergelic Cryaquepts	2.60
n=267[a]	Pergelic Cryumbrepts	2.60
	Histic Pergelic Cryaquepts	2.50
	Pergelic Cryoborolls	2.40
Subsurface Geology	Quaternary Mafic Volcanic Rocks - Basalt	1.00
n=182[a]	Ordovician Rocks - limestone and shale	1.00
	Precambrian Z undifferentiated volcanic rocks	0.90
	Upper Cretaceous Continental Deposits	0.85
Vegetation	Dwarf shrub tundra	0.35
n=24[a]	Alpine Tundra and Barrens	0.30
	Ocean Coast	0.30
	Tussock sedge/dwarf shrub tundra	0.28
	Tall shrub	0.28

[a] Denotes the total number of types within each predictor variable used for predictive modeling.

Table 2.4. Advantages of Modeling. Advantages of modeling over non-modeling approaches for predicting species occurrence and population size.

A) Quantitative.
B) Repeatable.
C) Objective.
D) Fast.
E) Convenient.
F) Nest distribution summarized by one algorithm.
G) Provides habitat response curves.
H) Includes multivariate interactions and responses.
I) Compilation of all relevant data into one dataset.
J) Brings experts together.
K) Stimulates discussion.
L) Improves hypotheses.
M) Broadly applicable across remote, inaccessible areas.
N) Represents best available science.
O) Represents complex interactions with simple numerics.

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Chapter 3. Detection Probability of Cliff-nesting Raptors During Helicopter and Fixed-wing Aircraft Surveys in Western Alaska. [1]

ABSTRACT

We conducted repeated aerial surveys for breeding cliff-nesting raptors on the Yukon Delta National Wildlife Refuge (YDNWR) in western Alaska to estimate detection probabilities of Gyrfalcons (*Falco rusticolus*), Golden Eagles (*Aquila chrysaetos*), Rough-legged Hawks (*Buteo lagopus*), and Common Ravens (*Corvus corax*). Using the program PRESENCE, we modeled detection histories of each species based on single species occupancy modeling. We used different observers during four helicopter replicate surveys in the Kilbuck Mountains and five fixed-wing replicate surveys in the Ingakslugwat Hills near Bethel, AK. During helicopter surveys, Gyrfalcons had the highest detection probability estimate ($\hat{p}$) ($\hat{p}$ =0.79 (SE 0.05)), followed by Golden Eagles ($\hat{p}$ =0.68 (SE 0.05)), Common Ravens ($\hat{p}$ =0.45 (SE 0.17)), and Rough-legged Hawks ($\hat{p}$ =0.10 (SE 0.11)). Detection probabilities from fixed-wing aircraft in the Ingakslugwat Hills were similar to those from the helicopter in the Kilbuck Mountains for Gyrfalcons and Golden Eagles, but were higher for Common Ravens ($\hat{p}$ =0.85 (SE 0.06)) and Rough-legged Hawks ($\hat{p}$ =0.42 (SE 0.07)). Fixed-wing aircraft provided detection probability estimates and SEs in the Volcanoes similar to or better than those

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[1] Booms, T.L., P.F. Schempf, B.J. McCaffery, M.S. Lindberg, and M.S. Fuller. 2010. Detection probability of cliff-nesting raptors during helicopter and fixed-wing aircraft surveys in western Alaska. Journal of Raptor Research, in press.

from helicopter surveys in the Kilbucks and should be considered for future cliff-nesting raptor surveys where safe, low altitude flight is possible. Overall, detection probability varied by observer experience and in some cases by study area/aircraft type.

INTRODUCTION

Accounting for imperfect detection is an important component of rigorous wildlife surveys (Burnham 1981, Yoccoz et al. 2001, Pollock et al. 2002, Buckland 2006, Johnson 2008). Observers will miss some, possibly many animals during most surveys, and the detection probability likely varies by a number of factors such as weather, vegetation, animal color, and observer experience (Bowman and Schempf 1999, Rosenstock et al. 2002). Because detection probability can vary spatially and temporally, failing to estimate and account for variation in detection probability can bias inferences from counts (Link and Sauer 1998, Eberhardt et al. 1999, Thompson 2002).

Most survey protocols attempt to control for some of these factors by limiting surveys to similar, optimal conditions (e.g., conducted during good weather and with trained observers; Johnson 2008) or by integrating measures of some variables in analyses of counts. However, it is unreasonable to assume all or even most of the factors influencing bird detection probability can be measured accurately or controlled or accounted for by using covariates or constants (Nichols et al. 2000, Diefenbach et al. 2003). Results of counts that do not incorporate estimates of undetected but present animals rely on the assumption that detection probability is 1.0 and that it is constant among surveys (e.g., locations, time), or that the variability in detection probability is negligible compared to the size of potential change in counts (Johnson 2008). Assuming constant or near constant detection probability is widely practiced; as evidenced in 95% of land bird surveys conducted between 1989 and 1998 (Rosenstock et al. 2002).

Imperfect detection is rarely accounted for in the majority of raptor survey methods (Andersen 2007), despite early examples with Ospreys (*Pandion haliaetus*) by Henny et al. (1977) and Bald Eagles (*Haliaeetus leucocephalus*) by Grier at al. (1981). This is particularly germane to raptor conservation because many species are uncommon,

elusive, or threatened, making population monitoring difficult and the application of rigorous survey techniques all the more vital (McDonald 2004). There have been some other examples of applying detectability estimates to different types of surveys and to several raptor species (e.g., Geissler and Fuller 1986, Anthony et al. 1999, MacKenzie et al 2003, Good et al. 2007, Henneman et al. 2007, Conway et al. 2008, Martin et al. 2009). However, we were unable to find published aerial detection probability estimates for cliff-nesting raptors during the breeding season even though aerial surveys are a commonly used technique for surveying raptors (Andersen 2007).

Therefore, we investigated the detection probability of cliff-nesting raptors during helicopter and fixed-wing surveys on the Yukon Delta National Wildlife Refuge (YDNWR) in May 2007. Our objectives were to 1) estimate the detection probabilities of Gyrfalcons (*Falco rusticolus*), Golden Eagles (*Aquila chrysaetos*), Rough-legged Hawks (*Buteo lagopus*), and Common Ravens (*Corvus corax*) during aerial surveys; 2) determine if detection probabilities were influenced by observers; and 3) evaluate the usefulness of fixed-wing aircraft in cliff-nesting raptor surveys.

METHODS

We conducted aerial surveys for raptors in two study areas on the YDNWR in western Alaska, the Kilbuck Mountains and the Ingakslugwat Hills (hereafter called 'the Volcanoes') in May 2007. The Kilbuck Mountains study area covers approximately 2,000 km^2, is located at approximately 60°21'N, 160°W, and includes much of the Kisaralik and Kwethluk river watersheds. The area consists of large, open valleys and low mountains reaching 975 m. Our focus was on cliff nests, and most cliffs are typically discrete rock faces less than 300 m in length that occur along river banks or on valley hillsides. Many of the cliffs in the headwaters occur in narrow canyons where access by fixed-wing aircraft is difficult or not possible. The study area supports relatively high numbers of breeding Gyrfalcons and Golden Eagles; lower numbers of Rough-legged Hawks and Common Ravens are present. For simplicity, we considered the Common Raven a cliff-nesting raptor because of its similarity in breeding biology to raptors and

the important role they play in creating and occupying cliff nests. The Kilbueks study area has been surveyed for eliff-nesting raptors on a mostly annual basis since 1977, and YDNWR maintains a GPS database of historical raptor nest sites.

The Volcanoes study area is dominated by small, inactive volcano craters typically less than 1 km wide and up to 200 m in elevation. The area is located at approximately 61°21'N, 164°W and covers 700 km^2. The Volcanoes study area is surrounded by the vast lowland deltas of the Yukon and Kuskowkim rivers, and provides the only cliff habitat for 90 km in any direction. The Volcanoes area was more conducive to fixed-wing aircraft surveys because the open landscape and low topography allowed for safer maneuvering among sites and lower flights over nesting habitat compared to the mountainous Kilbuck study area. The Volcanoes study area contains among the highest known nesting densities of Gyrfalcons (Booms et al. 2008) with a mean inter-nest distance of 4.7 km (BJM, unpubl. data). Rough-legged Hawks and Common Ravens also nest in large numbers in the area; Golden Eagle nest density is low relative to the other species in Volcanoes, and to eagle densities in the Kilbucks (BJM, unpubl. data). All species nest on the inner walls of the volcanoes, on small cliffs along the margins of lava flows, at isolated tors, and, with the exception of Golden Eagles and Rough-legged Hawks, occasionally in isolated stands of small balsam poplar (*Populus balsamifera*). BJM and YDNWR colleagues have surveyed cliff-nesting raptors in Volcanoes since 1988 and maintain a GPS database of historical nest sites.

General Survey Design

We followed the single species, single season study design for estimating detection and occupancy probability (MacKenzie et al. 2002, 2006). Gyrfalcons were our primary study species, and we designed the study to maximize the quality and quantity of data obtained for this species by surveying sites where Gyrfalcons had previously been observed breeding, by timing the surveys to coincide with the Gyrfalcon incubation period, and by using species-specific survey decision rules (see last paragraph below). We modeled data from all species simultaneously in our first modeling step to determine

if partitioning data by species and study area was justified (see Model Development below). Based on results from these models, we modeled data on each species separately.

We conducted four and five aerial surveys (hereafter referred to as replicate surveys) of historical raptor nest sites in the Kilbuck Mountains and Volcanoes study areas, respectively, in May 2007. During each replicate survey, we collected detection data for each raptor species at historical nest sites; a bird was detected or no bird was detected. We then created detection histories for each species across all sites and sampling occasions (MacKenzie et al. 2006).

We used the following terms and definitions throughout: *Survey Site* – is based on the location of a nest used previously by a raptor and marked with a GPS-obtained latitude and longitude accurate to within <20 m. All GPS locations were obtained in prior years from a helicopter hovering approximately 10-20 m from a nest. The site was considered occupied if a bird or egg was detected within approximately 500 m of the nest and this area served as our sampling unit. When multiple historical nests were located on a single cliff, we used only one GPS location to locate the survey site. *Detection probability (p)* – the probability of a species being detected at a site given the site is occupied. *Occupancy (ψ)* – the probability that the species of interest is present at a site during the survey period. A site was considered occupied if the species was detected there during any of the surveys; confirming breeding status was not necessary for us to consider a site occupied.

For a number of reasons we chose historical nests instead of random sites as the basis for our sample units and the starting point for each survey site. First, essentially all suitable nesting habitat in both studies areas had been previously surveyed and the resulting historical nests represented the majority of sites used by cliff-nesting raptors in the study areas. Second, we wanted to test this methodology and using historical nests provided us the largest sample sizes. Third, using nest GPS locations from historical databases allowed us to easily standardize methodology and served as a useful starting point for searching the survey unit. Last, the four raptor species used similar landscape

features in our study areas, which allowed us to gather useful information on all species at historical nests.

One of four observers, with varying amounts of experience, conducted each replicate survey. Each observer had previously conducted 2, 10, 20, or 53 aerial surveys for cliff-nesting raptors from helicopters. For modeling purposes, we considered the two observers who had conducted 2 or 10 surveys as *inexperienced observers* and the two observers who had conducted 20 or 53 surveys as *experienced observers.*

Replicate surveys in each study area were flown by the same helicopter or fixed-wing pilot to maintain consistency. Pilots did not participate in the survey other than by flying aircraft and were asked not to aid observers in detecting birds to ensure objective, independent survey replicates. Each observer conducted one replicate survey in each study area (except TLB conducted 2 surveys in the Volcanoes). To ensure surveys were independent, no survey results were shared among observers that might affect their search efforts.

To conduct a replicate survey, each observer used the same, pre-defined list of survey sites in a handheld GPS unit and used the GPS to navigate among sample units in the same order in each survey. All observers conducted replicate surveys according to the following decision rules: 1) If the GPS location was in front of a cliff, the survey team began surveying for raptors at the beginning of the cliff and made a slow pass in front of the entire cliff, passing through the GPS location. 2) If the GPS location was over a grove of trees, the team flew slightly to one side of the historical nest location. 3) If the GPS location was in a volcano crater, the team flew a straight line over the crater. 4) The team made three passes over all survey sites unless a Gyrfalcon was detected. Once a Gyrfalcon adult or egg was observed, no additional passes were made to minimize disturbance and reduce the likelihood of changing the birds' behavior in subsequent replicate surveys. If a species other than a Gyrfalcon was detected, the observer continued to survey the site until all three passes were completed. If an incubating Golden Eagle was detected, the observer continued to make passes in front of the site but remained at least 200 m (horizontal distance) from the nest to reduce

disturbance to the bird. Observers recorded the presence or absence of each species at each survey site, the number of birds detected, the behavior of birds detected, the pass on which they were detected, and relevant breeding information (e.g., clutch size).

Study Design by Study Area

Kilbuck Mountains

All replicate surveys in the Kilbuck Mountains were conducted with a Robinson 44 helicopter because the topography precluded safe, effective surveying with a fixed-wing aircraft. Helicopter ground speed while surveying at sites was dictated by wind conditions but was always <20 km/hr and often <5 km/hr. Replicate surveys were conducted on different days between 7 and 13 May 2007. We surveyed 83 sites during each of the four replicate surveys; six sites were not surveyed during one replicate because of fuel limitations. We used observations from all 83 sites for analysis.

Volcanoes

Replicate surveys in the Volcanoes were conducted with an Aviat Husky fixed-wing aircraft because the open terrain and landcover was conducive to less expensive fixed-wing surveys. Airplane ground speed and altitude during surveys varied with wind conditions, but was generally 100 km/hr and 20-100 m above the terrain (Ritchie et al. 2003). Replicate surveys were conducted on different days between 5 and 14 May 2007. We surveyed 46 sites in each replicate survey. During one replicate, 28 sites were missed because an inexperienced observer became air sick. Therefore, T. B. (experienced observer) conducted an additional replicate to ensure an adequate sample size; data from all 5 replicates and all 46 sites were analyzed.

Data Analysis

We used maximum likelihood estimation procedures in program PRESENCE 2.0 (Hines 2006) to obtain parameter estimates for ψ and p and followed recommendations by MacKenzie et al. (2002, 2006) and Burnham and Anderson (2002). We used model selection procedures (Burnham and Anderson 2002) to interpret Akaike's information criterion (AIC) values among competing models and report the parameter estimates and SEs from the model with the most AIC weight within each set of candidate models.

We used the "assess model fit" option in program PRESENCE for the most general model in each set of candidate models to calculate an overdispersion parameter estimate (c-hat) with 1,000 parametric bootstraps. We did this because most count data from ecological studies are likely to be over-dispersed, and statistical tests of ecological data with small sample sizes such as ours have little power to detect overdispersion (Burnham and Anderson 2002). Therefore, in model comparisons, we used the conservative quasi-Akaike's information criterion (QAIC) that was corrected by c-hat to account for potential overdispersion. If c-hat ≤ 1, we used c-hat =1 to calculate QAIC (Burnham and Anderson 2002). Though overdispersion is unlikely to bias parameter estimates, it is likely to affect the SE of estimates. Therefore, we also adjusted the SEs of parameter estimates by multiplying the model-based SE by the square root of c-hat (Burnham and Anderson 2002). We report all parameter estimates followed by overdispersion-corrected SE in parentheses. Because our sample sizes were small when data were partitioned by species and study area, we used $QAIC_c$ to account for small sample sizes when making model comparisons.

Our methods included the following analytical assumptions (MacKenzie et al. 2006): *1) Population of interest is closed during the sampling period.* This is a reasonable assumption for our work because we conducted all replicate surveys in the Kilbuck Mountains and Volcanoes within a 7 and 10-day period, respectively. However, we may have violated this assumption for Rough-legged Hawks because they might have been still searching for nest sites during our sampling period (see discussion below). We therefore interpreted results for this species in that context. *2) The probability of*

occupancy is the same at all sites. It is reasonable to expect that nest sites vary in quality and that higher quality sites might have a higher probability of occupancy. However, because historical data at our study sites were not collected with standardized efforts and methods that would have allowed us to assess occupancy probability at each site (largely because no detection probabilities could be estimated), we have no information with which to formally test this assumption. However, we believe potential variation in occupancy probability reflects natural variation that cannot be controlled or accounted for in many instances. The effect of violating this assumption is not well known, but it likely would have reduced the precision of our occupancy estimates (MacKenzie et al. 2006). Therefore, because violating this assumption would have only affected variation around occupancy estimates and because estimating occupancy was not a priority for this work anyway, we did not consider a potential violation of this assumption serious. *3) Detection probability is the same at all sites.* Site-specific differences such as cliff color or complexity may influence detection probability during aerial raptor surveys to some unknown degree. Also, we do not know if detection probability of raptors at cliff sites is similar to that of raptors at poplar groves (Volcanoes). We did not include nest site type as a covariate in our models because there were relatively few tree nests. Violating this assumption would primarily result in negatively biased occupancy estimates and increased variation around detection probability estimates (MacKenzie et al. 2006). Ideally, we would have conducted this work at a larger number of sites with similar variations in physical characteristics (cliff color, degree of over-hang, etc) and then use these variables as covariates to model potential variation in detection probability. However, given typical limitations in survey funding, sample size, and natural, nearly continuous variation in many cliff characteristics, this approach is unrealistic for our current circumstance and most we can envision. Therefore, we consider any increased error part of the natural variation that would be difficult to account for in most cliff-nesting raptor surveys. Further, SEs around many of our detection probability estimates were reasonable and do not suggest that a potential violation of this assumption seriously compromised our results. *4) The occupancy of a site is independent of the occupancy*

status of any other site. This assumption could be violated in two ways when working with territorial birds such as raptors. First, a bird could defend a territory that included multiple nest substrates and prevent those sites from being occupied by conspecifics. However, we do not know the size or configuration of territories in our study areas. Also, we note that, at least in the Volcanoes, the proximity of nests suggests that the area a bird defends is small. This assumption may also have been violated if birds were moving between historical nest locations and were detected at more than one site. This is unlikely, however, because raptors spend most of their time either hunting (in the case of the male) or occupying the nest cliff (Newton 1979). Violations of this assumption would have affected occupancy estimates. Future surveys that focus on estimating occupancy would need to ensure adequate and random spatial distribution of survey points to meet this assumption. Additionally, the potential effects of violating assumptions 2-4 on sampling variance estimates is at least partially accounted for by using c-hat to adjust variances.

Model development

Though we suspected *a priori* that analyzing data from each species in each study area separately would be the most biologically appropriate, we wanted to ensure that there was not more structure in the data than we suspected. Therefore, we combined all data across species and study areas and produced a candidate set of models using species, study area, observer experience, and all combinations of these covariates for p, and allowed ψ to vary by species and area (Table 3.1). We did not investigate ψ further because we considered it biologically unrealistic for occupancy not to vary by species and study area and because we were relatively uninterested in the complexity of ψ for this study. We then used standard model selection procedures to interpret ΔQAIC and QAIC weights among competing models and considered models with a $\Delta\text{QAIC} < 2$ as having substantial support (Burnham and Anderson 2002). Based on the resulting model QAIC weights, we then modeled data from each species in each study area separately and included observer experience as a covariate in all subsequent modeling.

We modeled each group of data with the following set of competing models:

$\psi(.),p(.)$ – Constant occupancy and detection probability.

$\psi(.),p$(experience) – Constant occupancy but detection probability varied by observer experience.

$\psi(.),p$(survey) – Constant occupancy but detection probability varied by survey.

RESULTS

When we combined all data, models with species as a covariate for p, including models that also had area, experience, or area and experience as covariates, received all of the QAIC weight (Table 3.1). Hence, partitioning data by species and study area for subsequent modeling was warranted, as was including experience as a covariate.

Detection probability estimates derived from models with the most support (Table 3.2) varied among species. Generally, Gyrfalcons were the most detectable, followed in order by Golden Eagles, Common Ravens, and Rough-legged Hawks (Table 3.3). However, detection probability of Rough-legged Hawks and Common Ravens differed greatly by study area/aircraft type. For example, Common Ravens, when surveyed by fixed-wing aircraft in the Volcanoes, were the most detectable of the four species at $\hat{p}$ =0.85 (SE 0.06). However, raven detection probability was much lower in the Kilbuck Mountains when surveyed by helicopters ($\hat{p}$ = 0.45 (SE 0.17)), although this might have been an artifact of the low number of detections in the Kilbucks (n=3).

Models with constant detection probability and those with observer experience as a covariate both received substantial support (Table 3.2). Models assuming constant detection probability always received more support, though the differences in $QAIC_c$ weights between observer experience and constant detection models within any suite of models varied from 0.01 to 0.47. Experienced observers had higher detection probability estimates than inexperienced observers for almost all species and study areas/aircraft types, though the differences were sometimes small (Table 3.3). There was relatively little support for different survey-specific detection probability for all species.

Though direct comparisons of detection probability estimates between aircraft type was not possible because they were confounded by study area, fixed-wing aircraft in the Volcanoes provided estimates of detection probability for Gyrfalcons and Golden Eagles similar to those from helicopter surveys in the Kilbucks (Table 3.3). Detection probability estimates for Common Ravens and Rough-legged Hawks, however, were higher in fixed-wing surveys. We suspect this may be at least partly due to the low number of detections for these species in the Kilbucks helicopter surveys, differences between study areas, and, for Rough-legged Hawks, possibly due to a violation of the assumption of population closure (see discussion below).

DISCUSSION

Our results showed detection probability for raptors at historical nest sites during helicopter and fixed-wing surveys in western Alaska differed by species, study area, aircraft, and observer experience. Commonly, survey results are used to compare the occurrence of animals among geographic areas or through time for the purpose of monitoring status. Our results demonstrate that several factors are associated with differences in the probability of observing raptors among surveys and thus are important for interpreting and comparing results.

Species Differences

Gyrfalcons were the focal species for these surveys, and the timing, design, and execution of the surveys were tailored to maximize the likelihood of detecting Gyrfalcons. It is therefore unsurprising that Gyrfalcons had some of the highest detection probability estimates ($\hat{p}$ =0.78 and 0.79). Had replicate surveys been conducted later in the breeding season, detection probability for other species might have been higher, especially in the case of Rough-legged Hawks, which breed later than Gyrfalcons and Golden Eagles. Also, because of species-specific survey decision rules, we conducted more survey passes when Gyrfalcons were not observed. These additional passes could have influenced differences among species detection probabilities if birds changed behavior during the

survey season because of repeated disruptions (passes). Last, we emphasize that the detection probability estimates presented here are likely minimum estimates because the pilot was not allowed to participate in the survey. We expect that detection probability would have been slightly higher had the pilots participated as is typically done during aerial surveys.

Surprisingly, our detection probability estimates for Rough-legged Hawks were lower than those for Golden Eagles. We expected Rough-legged Hawks to be more detectable than eagles because of the hawks' propensity to flush when disturbed and because of their contrasting wing and tail plumage patterns. We suspect that our estimates for Rough-legged Hawk detectability are biased low because their populations may not have been closed during our survey period and therefore violated a critical assumption of occupancy modeling. Two lines of reasoning support this hypothesis. First, Rough-legged Hawks are the last of the four species to initiate nesting on our study areas (TLB, BJM, unpubl. data). We failed to detect evidence of breeding (eggs or young) during many of our sightings of Rough-legged Hawks, even though we commonly detected evidence of breeding for the other species. Second, the number of sites at which Rough-legged Hawks were detected generally increased during our survey period in the Volcanoes and Kilbucks. Total counts of sites at which Rough-legged Hawks were detected during each replicate from earliest to latest calendar date were 9, 6, 10, and 14 in the Volcanoes (excluding the incomplete survey) and 1, 1, 2, and 4 in the Kilbucks. Based on these counts, Rough-legged Hawk occupancy appeared to increase during the survey period, probably because they were still in the process of choosing nest sites and initiating nesting. This likely caused a closure assumption violation and resulted in biased detection probability estimates for Rough-legged Hawks.

We attributed the high detection probability of ravens in the Volcanoes ($\hat{p}$ =0.85) to their conspicuous black plumage and use of nests in small, isolated, easily-surveyed poplar stands. Additionally, Common Ravens in the Volcanoes had a nesting phenology very similar to Gyrfalcons and the timing of the surveys was probably optimal for detecting ravens. We are unsure why detection probability of ravens was relatively low

in the Kilbucks, but this was perhaps a function of low occupancy (estimated 0.04) or more cryptic nest site placement than in the Volcanoes.

Except for Martin et al. (2009), we are unaware of detection probability estimates for these species or for cliff-nesting raptors in general during breeding-season surveys. For Golden Eagles breeding in Denali National Park, AK, Martin et al. (2009) estimated detection probabilities during a combination of repeated helicopter and ground-based surveys varied from 0.90-1.0. These estimates are higher than ours and the difference is most likely explained by their use of ground-based work to complement aerial surveys and by differences in study area and observer experience. We found no other estimates with which to compare ours or to investigate potential spatial, methodological, or temporal differences. This highlights a significant deficiency in and obstacle to the study and conservation of birds of prey (Anthony et al. 1999).

There are published studies that estimated detection probability of eagles, hawks, or owls during other types of surveys. For example, detection probability estimates of Red-shouldered Hawks (*Buteo lineatus*) varied from 0.11 to 0.45 among four study area (Iverson and Fuller 1991). Estimates for Spotted Owls (*Strix occidentalis*) during ground surveys of historical nesting areas ranged from 0.53-0.76, and varied widely, both temporally and spatially (Olson et al. 2005). Wintle et al. (2005) found that ground surveys for the Powerful Owl (*Ninox strenua*) and Sooty Owl (*Tyto tenebricosa*) in Australia produced low estimates of detection probability ($\hat{p} = 0.13$ and 0.26, respectively). Bald Eagle sightability estimates during fixed-wing aerial surveys in two areas in Oregon were 0.64 and 0.35, and sightability was lower during aerial surveys than during ground surveys (Anthony et al. 1999). Bowman and Schempf (1999) estimated detection probabilities for adult Bald Eagles at $\hat{p} = 0.79$ and for immature eagles at $\hat{p} = 0.51$ from fixed-wing aerial surveys during the breeding season in south-central Alaska. Good et al. (2007) conducted fixed-wing aerial line-transect surveys across the western United States for Golden Eagles after the breeding season and estimated the detection probability of perched eagles at $\hat{p} = 0.29$ and flying groups of eagles at $\hat{p} = 0.55$, though estimates varied with detection distance. Last, using broadcast call

surveys and program PRESENCE, Henneman et al. (2007) found Red-shouldered Hawks had an average detection probability of $\hat{p}$=0.38 across 4 years of breeding surveys and annual estimates varied from $\hat{p}$=0.28 to $\hat{p}$=0.54. Collectively, these studies highlight the need to account for detection probability during raptor surveys because probability of detection can vary widely by species, area, survey type, time, and other factors. It is possible that detection probabilities for cliff-nesting raptors may not change significantly across years if methods, good weather, and observers remain the same. Investigating this with additional work in our and other study areas would help identify the best balance between the need to account for detection probability and survey costs. Our findings with cliff-nesting raptors in western Alaska further support the need for more research on, and applications of, detection probability estimation in raptor surveys.

Observer Experience Differences

Although often only marginally better than competing models, models assuming constant detection probability received the most support. Models with observer experience as a covariate also received substantial and sometimes very similar amounts of support. Whether looking at the cumulative data set (Table 3.1) or individual species by study area data sets (Table 3.2), the majority of models that included observer experience as a covariate for detection probability received substantial support and sometimes nearly the same amount of support as the top model assuming constant detection probability. We interpret these results, along with the differences in experience-specific parameter estimates (Table 3.3), as indicating that observer experience generally influenced detection probability and this conclusion has been well documented in other bird surveys (Diefenbach et al. 2003).

However, observer experience may influence detection probability to a greater or lesser extent in different species. For example, Common Raven models that included observer experience as a covariate for detection probability did not receive substantial support (ΔQAICc = 2.02 and 2.15) while those for Gyrfalcons did (ΔQAICc = 0.05 and

0.45). Also, the difference in detection probability estimates between experienced and inexperienced observers was the least for Common Ravens (0.0 in helicopters and 0.07 in fixed-wing) and the most for Gyrfalcons (0.15 in helicopters and 0.21 in fixed-wing). We conclude Common Raven detection probabilities were the least affected by observer experience while those of Gyrfalcons were the most affected. Therefore, not only did detection probabilities differ among species, but the degree to which observer experience influenced detection probability differed among species.

Study Area/Aircraft Differences

We did not conduct helicopter surveys in the Volcanoes or fixed-wing surveys in the Kilbucks because of budgetary and logistical considerations. Therefore, direct comparisons of detection probability by aircraft type or between regions were not possible because aircraft type and study area were confounded. We conclude, however, that in the Volcanoes study area, fixed-wing aircraft generally provided detection probability estimates and SEs that were similar to or higher and more precise than those generated by helicopters in a different area (Table 3.3). Furthermore, fixed-wing surveys were much less expensive than helicopter surveys ($100/hr vs. $700/hr). Thus, we encourage the evaluation of the use of fixed-wing surveys in long-term raptor monitoring programs for estimating occupancy. Counting eggs or young is difficult from fixed-wing aircraft (TLB, BJM pers. obs.) and fixed-wing aircraft might be less suitable for surveying very rugged, mountainous terrain for obvious safety reasons. Our work demonstrates that at least for some applications, fixed-wing aircraft are a suitable survey platform for cliff-nesting raptor surveys.

Implications for Future Surveys

Conducting two repeat helicopter surveys may be prohibitively expensive for YDNWR and other organizations interested in population monitoring. If so, conducting repeat visits at only a subset of survey points may be possible and could allow detection

probability to be estimated. In areas that allow for safe maneuvering and low flight in a fixed-wing aircraft, planes may provide a more cost-effective option that would enable the YDNWR and others to fund future surveys on a long-term basis while still surveying in a rigorous, defensible manner.

In some situations, using a double-observer approach during a single survey as was done by Anthony et al. (1999) and Bowman and Schempf (1999) could be less expensive than replicated surveys. Unfortunately, helicopters and tandem-seat airplanes best suited for cliff-nesting raptor surveys do not provide multiple observers the same field of view and therefore are problematic for double-observer methods. Conducting repeated surveys was the only tenable option for estimating detection probability using the types of aircrafts most suited to cliff-nesting raptor surveys. Our results and those of others show that it is scientifically justified to expend the resources to account for imperfect detection during raptor surveys.

The YDNWR contains expanses of landscape in which cliff nesting raptors do not occur, thus a randomized survey design that encompassed all of the refuge would have been impractical to implement to cover enough nesting habitat to provide counts large enough to be useful. In our study, SEs for species detected at ≤ 5 sites were large. A design based on historical nest locations was suitable for our objectives as we described in the Methods section. However, survey objectives commonly require estimates that are representative of all nest sites in the area being sampled, not only information about historical nests. Information based only on historical nests is incomplete because not all nests have been discovered, some nests are abandoned, and new nests are established. Survey design also has important ramifications when distinguishing between the proportion of sites occupied and the probability of occupancy (ψ) (MacKenzie et al. 2006). Nevertheless, information about historical nesting, such as nest substrate, surrounding terrain, etc., can be used to develop a suitable design. An example of such a design is the dual frame method (Haines and Pollock 1998) comprising a list frame of all known nests in the study area and an area frame which delineates plots in which additional surveys for nests are conducted. The sample information from both frames is

combined to estimate the number of nests in the study area. Millar et al. (2007) applied the Haines and Pollock (1998) approach in a draft monitoring plan for Bald Eagles that included an estimate of detection probability using double-observer method described by Nichols et al. (2000).

Our results have important implications for raptor nest site surveys. First, we demonstrated that not all cliff-nesting raptors are detected during a survey and that detection probability was associated with a number of factors. Our results indicate the importance of estimating detection probability in future raptor surveys to allow for robust, reliable, scientific population monitoring across time and space. Second, we provided the first estimates of detection probability during aerial surveys for these four species of cliff-nesting raptors during the breeding season. These estimates can be used by others to guide the design of future surveys to estimate detection probability of raptors in other places and times. Though our estimates cannot be generalized across time or space, replicating this study at this and other study sites would assess the degree of generality among species-specific estimates of detection probability. If similar detection probabilities are repeatedly documented, there might be a basis for estimating this parameter less often than during each survey period. Such a finding also could increase our ability to interpret trends in survey data. Third, we demonstrated that accounting for imperfect detection probability was possible even in remote, logistically difficult study areas; doing so is likely feasible in other challenging study areas. Fourth, fixed-wing aircraft were an effective, comparatively inexpensive survey platform in a study area that allowed for safe, very low altitude flying; they deserve additional consideration by others planning aerial raptor surveys in areas that allow use of fixed-wing aircraft.

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Table 3.1. Model Selection Results from Pooled Data. Data pooled across species and area from aerial cliff-nesting raptor surveys on the Yukon Delta National Wildlife Refuge, Alaska in 2007.

Model	QAIC[a]	Δ QAIC[b]	QAIC wt[c]	No. of Parameters
ψ(species + area) *p* (species)	449.56	0.00	0.40	9
ψ(species + area) *p* (species + area)	449.97	0.40	0.32	10
ψ(species + area) *p* (species + experience)	451.43	1.87	0.16	10
ψ(species + area) *p* (species + area + experience)	451.92	2.36	0.12	11
ψ(species + area) *p* (.)	462.18	12.61	0.00	6
ψ(species + area) *p* (area)	463.95	14.39	0.00	7
ψ(species + area) *p* (experience)	464.18	14.61	0.00	7
ψ(species + area) *p* (area + experience)	465.93	16.37	0.00	8

[a]QAIC is the c-hat adjusted Akaike Information Criterion score to compensate for overdispersion, c-hat = 2.1.

[b]Δ QAIC is the difference between a model's QAIC score and the lowest QAIC score in the suite of models.

[c]QAIC wt is the relative weight of evidence for the model.

Table 3. 2. Model Selection Results by Species. Data from repeated aerial surveys of breeding cliff-nesting raptors on the Yukon Delta National Wildlife Refuge, Alaska in 2007. Data from each species in each study area were modeled seperately.

Model	$QAIC_c$[a]	$\Delta QAIC_c$[b]	$QAIC_c$ wt.[c]	Number of Parameters	c-hat[d]
Gyrfalcon - Volcanoes					
$\psi(.),p(.)$	92.88	0.00	0.47	2	1
$\psi(.),p$ (exp)	92.93	0.05	0.46	3	1
$\psi(.),p$ (survey)	96.88	4.00	0.06	6	1
Gyrfalcon - Kilbucks					
$\psi(.),p(.)$	129.57	0.00	0.53	2	1.1
$\psi(.),p$ (exp)	130.04	0.47	0.42	3	1.1
$\psi(.),p$ (survey)	134.04	4.47	0.06	5	1.1
Golden Eagle - Volcanoes					
$\psi(.),p(.)$	54.14	0.00	0.65	2	1.2
$\psi(.),p$ (exp)	56.20	2.06	0.23	3	1.2
$\psi(.),p$ (survey)	57.64	3.50	0.11	6	1.2
Golden Eagle - Kilbucks					
$\psi(.),p(.)$	182.87	0.00	0.49	2	1.1
$\psi(.),p$ (exp)	183.04	0.17	0.45	3	1.1
$\psi(.),p$ (survey)	186.82	3.95	0.07	5	1.1
Rough-legged Hawk - Volcanoes					
$\psi(.),p(.)$	117.62	0.00	0.61	2	1.6
$\psi(.),p$ (exp)	118.78	1.17	0.34	3	1.6
$\psi(.),p$ (survey)	122.65	5.04	0.05	6	1.6
Rough-legged Hawk - Kilbucks					
$\psi(.),p(.)$	56.69	0.00	0.65	2	1.4
$\psi(.),p$ (exp)	58.30	1.62	0.29	3	1.4
$\psi(.),p$ (survey)	61.29	4.60	0.06	5	1.4
Common Raven - Volcanoes					
$\psi(.),p(.)$	75.18	0.00	0.73	2	1
$\psi(.),p$ (exp)	77.20	2.02	0.26	3	1
$\psi(.),p$ (survey)	83.74	8.56	0.02	6	1
Common Raven - Kilbucks					
$\psi(.),p(.)$	46.10	0.00	0.71	2	1
$\psi(.),p$ (exp)	48.25	2.15	0.24	3	1
$\psi(.),p$ (survey)	51.50	5.40	0.05	5	1

[a] $QAIC_c$ is the Akaike Information Criterion corrected for small sample size and for potential overdispersion using c-hat.

[b] $\Delta QAIC_c$ is the difference between a model's QAICc score and the lowest QAICc value in the suite of models.

[c] $QAIC_c$ wt is the relative weight of evidence for the model.

[d] C-hat estimates < 1 were set equal to 1.

Table 3.3. Detection Probability Estimates. Data for each species by study area and aircraft type on the Yukon Delta National Wildlife Refuge, Alaska in 2007. Detectability estimates for experienced and inexperienced observers provided from models assuming detectability varied by observer experience (p (experience)).

Species	Study Area/Aircraft	Model	Detectability ($\hat{p}$)	Experienced Observer Detectability ($\hat{p}$	Inexperienced Observer Detectability ($\hat{p}$	Total Number of Sites Species was Detected
Gyrfalcon	Kilbucks - Helicopter	$\psi(.)\,p(.)$	0.79 (0.05)[a]	-	-	14
		$\psi(.)\,p$(experience)	-	0.87 (0.06)	0.72 (0.08)	14
	Volcanoes - Fixed-wing	$\psi(.)\,p(.)$	0.78 (0.07)	-	-	9
		$\psi(.)\,p$(experience)	-	0.85 (0.07)	0.64 (0.13)	9
Golden Eagle	Kilbucks - Helicopter	$\psi(.)\,p(.)$	0.68 (0.05)	-	-	20
		$\psi(.)\,p$(experience)	-	0.75 (0.08)	0.60 (0.09)	20
	Volcanoes - Fixed-wing	$\psi(.)\,p(.)$	0.69 (0.10)	-	-	5
		$\psi(.)\,p$(experience)	-	0.73 (0.13)	0.62 (0.18)	5
Rough-legged Hawk	Kilbucks - Helicopter	$\psi(.)\,p(.)$	0.1 (0.11)	-	-	5
		$\psi(.)\,p$(experience)	-	0.15 (0.16)	0.08 (0.10)	5
	Volcanoes - Fixed-wing	$\psi(.)\,p(.)$	0.42 (0.07)	-	-	20
		$\psi(.)\,p$(experience)	-	0.53 (0.12)	0.40 (0.08)	20
Common Raven	Kilbucks - Helicopter	$\psi(.)\,p(.)$	0.45 (0.17)	-	-	3
		$\psi(.)\,p$(experience)	-	0.45 (0.21)	0.45 (0.22)	3
	Volcanoes - Fixed-wing	$\psi(.)\,p(.)$	0.85 (0.06)	-	-	8
		$\psi(.)\,p$(experience)	-	0.90 (0.09)	0.83 (0.08)	8

[a] SE in parenthases corrected by multiplying model-based SE's by square root of c-hat for each model set (Table 3.2).

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Chapter 4. Direct and Indirect Estimates of Gyrfalcon Nest Site Fidelity and Breeding and Natal Dispersal using Non-invasive Genetic Sampling.[1]

ABSTRACT

We used molted feathers from adult Gyrfalcons (*Falco rusticolus*) collected in breeding territories and blood samples from nestlings to document nest site fidelity and breeding and natal dispersal at three study areas located 100-250 km apart on the Yukon Delta National Wildlife Refuge, Alaska, from 2003-2007. We used genotypes from seven polymorphic microsatellite loci that provided a mean probability of identity (unbiased P_{ID}) of 0.91 $x10^{-5}$. Gyrfalcons were highly faithful to study area and territories (98% breeding territory fidelity); we documented no breeding dispersal events among study areas and only one dispersal event between territories. Gyrfalcons exhibited low nest site fidelity; only 22% of birds returned to the same nest site the following year. The remaining 78% moved 50 - 3,400 m from the previous alternate nest site. Dispersal distance averaged 750 ± 870 m (SD), and was similar between sexes (females 754 ± 950 m (SD), $n = 19$; males 745 ± 740 m (SD), $n = 10$). Mean territory tenure was 2.8 ± 1.4 years, was similar between sexes (males 2.6 ± 1.3 years (SD), females 2.9 ± 1.6 years (SD)), and displayed a bimodal distribution with peaks at 1 and 4 years. Mean annual turnover rate at the Volcanoes study area was 20%. We detected three natal dispersal events ranging from 0 - 254 km representing 2.5% recruitment of the 121 sampled nestlings. Gyrfalcons in the Askinuk Moutains study area showed low, but statistically significantly differentiation from conspecifics in the Volcanoes and Kilbuck Mountain

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[1] Booms, T., S. Talbot, K. Sage, K. McCracken, B. McCaffery, and P. Schempf. Direct and indirect estimates of Gyrfalcon nest site fidelity and breeding and natal dispersal using non-invasive genetic sampling. Condor, in preparation.

study areas (F_{ST} = 0.04 and 0.07, $P < 0.01$, R_{ST} = 0.21 and 0.33, respectively, $P < 0.001$). We detected no significant genetic structure between Gyrfalcons in the Volcanoes and Kilbucks study areas and documented one natal dispersal event with a known individual between these study areas, corroborating genetic exchange. These data are the first published on nest site fidelity, breeding dispersal, and natal dispersal of Gyrfalcons in North America.

INTRODUCTION

Dispersal is one of the most important life history traits determining a species persistence and evolution (Hanski 1999, Wiens 2001) and includes both breeding (movement between breeding locations) and natal dispersal (movement from natal origin to location of first breeding) (Greenwood and Harvey 1982). Natal and breeding dispersal directly influence a wide range of important processes and individual qualities including gene flow and genetic diversity (Comins et al. 1980), fitness (Hansson et al. 2004), population distribution and range expansion/contraction (Lester et al. 2007), metapopulation dynamics (Gilpin and Hanski 1991), and speciation (Price 2008). Understanding dispersal (or lack thereof, fidelity) is therefore important to species conservation and management because the above processes and qualities can directly affect a species' population size, conservation status, vulnerability to extirpation, and resiliency (Fahrig and Merriam 1994, Pearce and Talbot 2006, Davis and Shaw 2001, Alcaide et al. 2009). However, dispersal is difficult to study (Turchin 1998) and is often considered one of the most significant knowledge gaps in ecological processes and species biology (Bennetts et al. 2001, Wiens 2001). This is especially so for highly mobile, long-lived species and those that are relatively uncommon or elusive, including raptors (Jenkins and Jackman 1993, Linkhart and Reynolds 2007).

Most raptors are believed to exhibit high breeding territory fidelity (Jenkins and Jackman 1993, Rosenfield and Bielefeldt 1996, Steenhof et al. 2005, Linkhart and Reynolds 2007). Raptors return to good quality, familiar sites because habitat and mate familiarity can increase breeding success (Newton 1979, Rowley 1983, Bradley et al.

1990, Reese et al. 1996). However, dispersal in some instances can also be beneficial by allowing individuals to respond to variable habitat, breeding density, and inbreeding depression (Clobert 2001).

The Gyrfalcon (*Falco rusticolus*) is the largest falcon species and breeds at low densities across Arctic portions of the circumpolar north (Booms et al. 2008a). The current population estimate for Alaska is 375 - 635 (Swem et al. 1994, Booms et al. 2009), and the world population is thought to be 8,000 - 11,000 pairs. They have large home ranges and can undergo long distance, intra and inter-continental movements >1,000 km (Burnham 2007, McIntyre et al. 2009). They are known to live at least 12 years in the wild (Cade et al. 1998), and captive birds have lived substantially longer (Booms et al. 2008a). Some historical nest sites have been used repeatedly for centuries (Burnham 2007), but information about individual fidelity to nest sites and territories and use patterns of alternate nests is generally unknown. Anecdotal observations of uncommon color variants and fidelity of two marked females in Iceland (Nielsen 1991) suggest that some individuals may remain faithful to nest sites. However, no other published data are available and, to our knowledge, none exist in the literature on dispersal or site fidelity of marked birds in North America or anywhere outside of Iceland.

Mark and recapture techniques with color bands and telemetry have been inadequate to address Gyrfalcon fidelity and dispersal. This is because observers are rarely present near remote Gyrfalcon nests to re-sight color bands and even if birds are observed, bands are often obscured by leg feathers making band reading difficult (TLB pers. obs.). Although satellite telemetry has elucidated movements of numerous species (Meyburg and Fuller 2007), it has yet to provide a single data point for Gyrfalcon nest fidelity or breeding dispersal and has some important limitations (Lindberg and Walker 2007). For example, Burnham (2007) placed satellite transmitters on 55 Gyrfalcons in Greenland but was unable to document site fidelity, breeding dispersal, or natal dispersal because signals were typically lost in less than a year.

Non-invasive genetic samples used in a mark-recapture context allow researchers to investigate dispersal, fidelity, and other fundamental aspects of a species' life history that were previously not possible (Taberlet and Luikart 1999, Bayard DeVolo et al. 2005, Waits and Paetkau 2005). Though non-invasive genetic sampling is common in mammalogy (Waits and Paetkau 2005, Prugh et al. 2005, Robinson et al. 2009), its use in ornithology is still rare (Morrison and Wood 2009). However, the technique holds tremendous potential for avian research because molted feathers can be easily and routinely collected, unique genotypes identified, and individuals followed temporally and spatially to investigate movements and other topics (Bayard DeVolo et al. 2005, Rudnick et al. 2008). Therefore, as part of an ongoing study of Gyrfalcon breeding biology, we collected molted feathers near nests and blood samples from nestlings at three studies areas on the Yukon Delta National Wildlife Refuge (Yukon Delta NWR) in western Alaska from 2003 - 2007. Our objective was to document and describe patterns of adult Gyrfalcon nest site fidelity, breeding dispersal, and natal dispersal for the first time in North America using 5 years of non-invasive genetic data.

METHODS

Study Area

We collected genetic samples from Gyrfalcons in three study areas on the Yukon Delta NWR: Ingakslugwat Hills (hereafter called the Volcanoes), Askinuk Mountains, and Kilbuck Mountains (Figure 4.1). The Volcanoes (61°21'N, 164°W) was our primary study area and is approximately 600 km^2 in size. It is dominated by small, inactive volcano craters typically less than 1 km wide and rising up to 200 m in elevation. The study area is surrounded by the vast lowland deltas of the Yukon and Kuskokwim Rivers, and almost no cliff-nesting habitat is available for approximately 70 km in any direction. The volcanoes, associated lava flows, and several isolated stands of balsam poplars (*Populus balsamifera*) serve as the only nesting substrate for Gyrfalcons in the area. The study area contains among the highest nesting densities of Gyrfalcons ever documented with a mean inter-nest distance of 4.7 km (BJM unpubl. data). Typically, there are 7 - 9

occupied Gyrfalcon territories annually and most of these successfully produce young (TLB unpub. data). We collected molted feathers from this study area in 2003 - 2007 and nestling blood samples in 2004 - 2007 (Table 4.1).

The Askinuk Mountains study area (61° 45'N, 164° 45' W) is located 100 km to the northwest of the Volcanoes across the lowland delta of the Yukon River and is a small mountain range on the coast of the Bering Sea with a maximum elevation of 700 m (Figure 4.1). Surrounding the study area on three sides are highly productive wetlands that support large numbers of breeding geese, ducks, and shorebirds. The area includes approximately 1,000 km^2 of rolling upland tundra. Gyrfalcons and other raptors nest on numerous isolated torres reaching up to 80 m in height that are scattered throughout the study area. Like the Volcanoes study area, the Askinuks is essentially an island of breeding habitat surrounded by wetland tundra or water. Though potential nest cliffs in the Askinuks are more numerous than in the Volcanoes, the cliffs are more dispersed and mean inter-nest distance is higher (8.5 km; BJM, unpub. data). We collected molted feathers and nestling blood samples from this study area in 2006 and 2007 (Table 4.1).

The Kilbuck Mountains study area (60°21'N, 160°W) is approximately 250 km southeast of the Volcanoes and 350 km from the Askinuks. The area is separated from the Volcanoes and Askinuks by a vast expanse of wetland tundra and boreal forest with essentially no cliff-nesting habitat in between (Figure 4.1). The study area covers approximately 2,000 km^2 and includes much of the Kisaralik and Kwethluck River watersheds. The area consists of large, open valleys and low mountains reaching up to 975 m in elevation. The Kilbucks study area is immediately surrounded by large tracts of cliff-nesting habitat that supports additional breeding Gyrfalcons. The mean inter-nest distance is 6.9 km (BJM, unpub. data). The cliffs are generally larger, more numerous, and more complex than those in the other study areas, and we were able to find relatively few feathers at territories because of this. Molted feathers and nestling blood samples were collected in the Kilbucks in 2005 and 2006.

Definitions of Terminology

Territory was defined as an area surrounding an occupied nest site in which no other breeding Gyrfalcons were observed concurrently during our study or historical surveys (Newton and Marquiss 1982). Nest sites within a territory used by resident birds were considered alternate nests. *Occupied* referred to having one or more adults observed or detected at a territory, regardless of breeding status. *Active* nests contained eggs or young. A *Unique Individual* was a bird represented by a consensus genotype that was independently obtained from 5 or more feather samples or, if obtained from 2 - 5 samples, differed from other genotypes by at least two alleles and was considered a resident. A *Resident bird* was a unique individual detected at a territory for which at least one of the following conditions was met: A) It was the only individual of that sex detected at a territory that year, B) It was a parental match to the genotype of nestlings present, C) If no nestlings were sampled, it was the most numerous adult genotype of that sex detected in feathers at that site that year, D) It was defending young and its color band was read confirming identity. *Occasion* refers to the detection of a unique individual at one territory in one year, regardless of the number of samples in which it was detected that year. *Old feathers* were those that were molted during the previous breeding season, over-wintered in the study area, and were distinguishable from fresh feathers by the presence of mold, algae, or highly separated barbs (Booms et al. 2008b). *Fresh feathers* were those that were molted during the current breeding season and lacked obvious mold, algae, or highly separated barbs (Booms et al. 2008b). *Annual Turnover* was the number of occasions in which an adult was known to be replaced on a territory divided by the total number of occasions for which adult identity at a territory was known in consecutive years (Linkhart and Reynolds 2007). *Territory tenure* was the total number of consecutive years that a unique individual occupied the same territory during our five-year study (Linkhart and Reynolds 2007). *Dispersal Distance* is the straight-line distance between consecutive nests or between a natal nest and place of first breeding as measured by a GPS.

Sample Collection

Gyrfalcons breeding below 70°N are thought to be non-migratory (though see Burnham 2007) and, based on movements from two adults harnessed with satellite transmitters in the Volcanoes study area, Gyrfalcons on the Yukon Delta NWR likely reside on their territories year-round (PFS unpub. data). In Alaska, Gyrfalcons begin molting feathers in early or mid-April during courtship, continue molting more or less continually throughout the breeding season, and complete molt in mid-late September, though differences exist between sexes and feather tracts (Booms et al. 2008a). Hence, molted feathers from breeding pairs can be commonly found near Gyrfalcon nests beginning in April and continuing through the breeding season. The ability to find feathers is dependant upon vegetation, cliff composition, location of perch sites, and presence of swallows that remove feathers for nest lining (TLB pers. obs.).

We attempted to collect molted adult Gyrfalcon feathers from perches, nests, and below nests at all known occupied Gyrfalcon territories in our study areas. Collection timing varied across years and study areas. In 2003, territories in the Volcanoes were visited after young had fledged. From 2004 - 2006, feathers were collected at territories in the Volcanoes multiple times opportunistically from pre-incubation (April) to post-fledging (July). In 2007, we collected feathers at the Volcanoes multiple times opportunistically during incubation (May) and nestling phases (June). Sites in the Askinuks and Kilbucks were visited only once in late June to collect molted feathers and nestling blood samples. We collected blood quills or blood from the brachial vein of nestlings in all study areas following common avian blood sampling protocols (Monk and Forbes 2007). Blood was stored in lysis buffer (Longmire et al. 1988) at ambient temperature while in the field and then frozen at – 80° C until DNA was extracted. Feathers were placed in individual paper envelopes stored in Ziploc bags containing silica desiccant until DNA was extracted. Because Rough-legged Hawks, Golden Eagles, and Peregrine Falcons occurred in the study areas, molted feathers were identified to species visually using size and plumage patterns in the field. All non-Gyrfalcon samples were separated and archived.

We captured five adult breeding Gyrfalcons in the Volcanoes, banded each with a uniquely coded color band, and drew blood from each for genetic identification. Subsequent re-sighting of two of these individuals and collection of their feather samples over four years of the study provided independent tests of genetic identification. We harnessed three of the captured adults with transmitters. One female died and was recovered the following year. A second female disappeared after approximately four months. The third female slipped its harness and was re-sighted as a breeding bird the following year. Because we do not know how transmitters affected the fate of the first two birds, we excluded them from all analyses. Data from males and females were treated independently throughout. Because most nests were not visited after late June, nest fate was unknown in most instances.

Whole genomic DNA was extracted from each blood and blood quill sample using protocols described in Medrano et al. (1990) and modified by substituting 0.7 volumes of 2-propanol in place of two volumes of ETOH. DNA was extracted from feathers using the same protocol, with the following exceptions: 1) dithiotrhreitol (0.1mg/mL) was added to the lysis buffer; 2) 1% glycogen was added to the DNA precipitation step; and 3) lysis proceeded for up to 5 days. Genomic DNA extractions were quantified using fluorometry and diluted to 50ng/μL working solutions.

Microsatellite DNA Genotyping and Molecular Sexing

Samples were genotyped at each of seven autosomal microsatellite loci using primers developed specifically for Peregrine Falcons and known to be polymorphic in Gyrfalcon populations: NVHfp, 13-1, 34, 54, 79-4, 82-2, 89-2, 92-1 (Nesje et al. 2000, Nesje and Roed 2000). Genotyping via the polymerase chain reaction (PCR) and visualization procedures were similar to those reported in Sonsthagen et al. (2004) for microsatellite loci. For quality control purposes, 10% of the samples were extracted, amplified, and genotyped in duplicate.

We determined the sex of each bird using PCR amplification of the CHD gene, using protocols similar to those outlined in Handel et al. (2006) and the P8/P2 primer set

(Griffiths et al. 1998). In Gyrfalcons, the reaction yielded a 403 base-pair (bp) product from the Z-chromosome (both males and females) and a 424 bp product from the W-chromosome (females only). We assigned sex based on the absence (male: ZZ) or presence (female: ZW) of the W-chromosome PCR product.

Data Processing

Feathers contain small amounts of DNA and are prone to genotyping errors including allelic dropout, false alleles, and scoring errors (Waits and Paetkau 2005, Hogan et al. 2007). Such errors can significantly affect individual classification and cause an excess of genotypes to be observed (Lukacs and Burnham 2005). To avoid including erroneous genotypes in analyses, we followed a conservative approach, strict laboratory procedures with liberal culling of samples, and published guidelines as suggested by Waits and Paetkau (2005). Because we were not interested in estimating the number of individuals present in samples, we took an even more conservative approach by only using genotypes that were found in multiple independent samples. Using independently replicated consensus genotypes increases the probability of accurate genotypes (Waits and Paetkau 2005). Therefore, all genotypes detected in five independent samples were accepted as correct. Genotypes replicated in 2 - 5 samples ($n = 11$) were accepted only if they differed from all other genotypes by two or more alleles. Because genotyping error is expected to occur randomly, the probability of observing the same errors at multiple loci in multiple samples is low (Waits and Leberg 2000). Hence, our dataset is an overly conservative representation of the number of birds present in our samples, but this provided us high confidence in the accuracy of the individuals used to assess dispersal and fidelity.

Genetic Diversity

Genetic diversity levels and probability of identity were calculated from a sample of nestlings (one nestling per nest) pooled from the three study areas. Mean number of

alleles (A) and observed and expected heterozygosities (H_O and H_E) were calculated in GENEPOP ver. 3.3 (Raymond and Rousset 1995). Each microsatellite locus in the putative populations (Askinuks, Volcanoes, and Kilbucks) was tested for deviation from Hardy-Weinberg equilibrium (HWE), using the Markov chain parameters provided (dememorization number = 10000, number of batches = 100, and number of iterations per batch = 5000). Since loci were not mapped to chromosomes, each pair of loci within each population was tested for linkage disequilibrium (LD) in GENEPOP using the Markov chain parameters provided.

Individual Identification and Relatedness

We identified matching, seven-locus genotypes from those obtained from all molted feathers using Microsatellite Toolkit (Park 2001). After testing the loci for linkage disequilibrium and Hardy-Weinberg equilibrium (HWE), we used the software GIMLET ver. 1.3.2 (Valière 2002), to calculate $P_{(ID)}$ and $P_{(ID\mathit{sib})}$ values to determine the probability of detecting individuals within each population. Nestlings (one per nest) from all populations were pooled for these analyses. $P_{(ID)}$ is the probability that another individual with the same genotype would be observed, given the sample frequency of the alleles observed at those loci, within the target population. $P_{(ID\mathit{sib})}$ estimates the probability of observing identical multilocus genotypes between two individuals sampled from a population comprised of first-order relatives (e.g., between siblings or between parent-offspring). General guidelines for identifying individuals using microsatellite loci suggest using a suite of markers that achieves a reasonably low $P_{(ID)}$ bounded between 0.0100 and 0.0001; $P_{(ID\mathit{sib})}$ provides a conservative upper bound on this estimate (Waits et al. 2001). We used Queller and Goodnight's (1989) relatedness (r_{xy}), as implemented in the program IDENTIX (Belkhir et al. 2002), to determine the average level of relatedness within eight pairs of resident birds in the Askinuks and eight in the Volcanoes.

Population Differentiation

Spatial variation in allelic frequency among the Askinuks, Volcanoes, and Kilbucks was assessed using *F*- and *R*-statistics, which describe the apportionment of allelic variance among individuals within and among populations, respectively (Wright 1951, Weir and Cockerham 1984, Slatkin 1995). Multilocus estimates of F_{ST} and R_{ST} were obtained using FSTAT and ARLEQUIN (Excoffier et al. 2005), using 18, 25, and 8 unique individuals to represent the Askinuks, Volcanoes, and Kilbucks study areas, respectively. We used Hedrick's (1999, 2005) method to calculate the maximum value of F_{ST} obtainable using the microsatellite loci, and significance was assessed in ARLEQUIN using 10,000 random permutation tests, whereby alleles were randomly permutated between two populations. Bonferroni corrections factors were employed to evaluate significance for multiple comparisons.

Because R_{ST} assumes a stepwise mutation model of microsatellite mutation, *R*-statistics are considered more appropriate than *F*-statistics, which assume an infinite-alleles model (Slatkin 1995). However, for populations that are still very recently diverged and/or connected via ongoing gene flow, *F*-statistics generally provide better estimates of differentiation than *R*-statistics because migration and drift are relatively more important forces acting on the populations than is mutation (Slatkin 1995).

Statistical Analysis

We used Mann-Whitney U tests executed in Statistics Online Computational Resource (Dinov 2006) to determine if males and females were detected in equal numbers in feather samples, if dispersal distance differed between study areas, and if pairwise relatedness of resident birds differed between study areas. We collected relatively few feathers from nest sites in the Kilbucks, and no adults were detected in multiple years there. Hence, data from this area were not included in analyses unless stated. Only data from the Volcanoes were used to assess tenure and turnover because other areas were sampled in only two years. We reported all results as mean ± SD and consider results significant at $P = 0.05$.

RESULTS

Feather and Blood Samples

We collected 1,347 adult molted feathers from 67 of 70 occupied territories (Table 4.1). From these, we detected 43 unique individuals in 570 feathers that we classified as resident birds in the Askinuks and Volcanoes study areas across all years. The number of males and females detected were similar (Table 4.2). Though additional individuals were detected in feather collections, they failed to meet the definition of a unique individual or were not considered a resident bird and were excluded from the analyses. The number of feathers in which individuals were detected at a territory each year varied greatly (Figure 4.2). Males were detected in fewer feathers per site per year than females (males 3.7 ± 3.0, $n = 36$; females 8.2 ± 7.2, $n = 52$; U = 557 $P < 0.001$). We collected blood samples from 121 nestlings from 44 of 54 known broods across all years and study areas (Table 4.3).

Microsatellite Loci and Relatedness

The mean number of alleles per locus for the pooled nestling samples was 5.6 and ranged from 4 to 11. Observed and expected heterozygosity were 45.6% and 50.2%, respectively. No significant deviations from HWE for the pooled samples were observed for any locus ($P = 0.069$ to 1.000) or overall ($\chi 2 = 9.682$, df = 14.0, $P_{global} = 0.785$). Linkage disequilibrium was detected at three locus comparisons (FP13 – FP34; FP13 – FP79; FP34 – FP92-1) among a total of 21 comparisons, which was higher than expected at random (Ps > 0.01). Subsequent analyses of data by population, rather than pooled, failed to detect a signature of LD, suggesting that the observed LD was due to admixture of samples from individuals representing more than one discrete population.

The suite of seven loci gave us a mean probability of incorrectly assigning a feather to an individual (unbiased P_{ID}) = 0.91 x10^{-5} (Table 4.4). Mean r_{xy} pairwise relatedness from 16 pairs of resident birds was - 0.80 ± 0.48. Thus, using P_{ID} was

appropriate because unique individuals did not appear to be closely related. Pairwise relatedness of resident pairs was not significantly different between the Askinuks (-0.94 ± 0.47, $n = 8$) and Volcanoes (-0.66 ± 0.47, $n = 8$; $U = 19$, $P = 0.172$).

Fidelity and Population Differentiation

We detected 24 individuals at active territories in multiple years on 60 occasions in the Askinuks and Volcanoes study areas. On nine additional occasions, we detected one of these individuals at a territory containing no eggs or young. We determined the location of consecutive nests from the 24 individuals on 37 occasions. Birds returned to the same nest in the following year in only eight instances (22%). Males and female were each responsible for four of these instances. Of the 46 occasions for which we could ascertain fidelity to a territory in consecutive years, birds returned to the same territory on 45 occasions (98% territory fidelity). Over the five-year study period in the Volcanoes, mean territory tenure was 2.8 ± 1.4 yrs, was similar between sexes (males 2.6 ± 1.3 yrs, females 2.9 ± 1.6 yrs), and displayed a bimodal distribution with peaks at one and fout years (Figure 4.3). Mean annual turnover rate at the volcanoes was 20%.

We detected low, but statistically significant differentiation (both *Fst* and *Rst*) between birds in the Askinuks study area and those in the other two study areas (Table 4.5). Differentiation was not significant between the Volcanoes and Kilbucks.

Breeding Dispersal

Individuals moved to a new nest in 29 of the 37 occasions (78%), and the proportion of females using new nests (83%) was slightly higher than that of males (71%). Movement distances ranged from 50 - 3,400 m, averaged 750 ± 870 m, and were similar between sexes (females 754 ± 950 m, $n = 19$; males 745 ± 740 m, $n = 10$). The longest distance moved between alternate nest sites within a territory was 2,300 m. Though not statistically significant, mean distance moved in the Askinuks (1725 ± 1080 m, $n = 4$) appears to be greater than that in the Volcanoes (595 ± 745 m, $n = 25$; $U = 22.5$, $P =$

0.08). We detected one dispersal event between territories in which a female in the Volcanoes moved 3,400 m to a territory where the resident female had died the previous winter (death confirmed via telemetry). We detected no other dispersal events between territories and no breeding dispersals among study areas. There were six occasions in which we detected an individual the year after they did not breed or their nest failed. In all instances, the bird returned to breed in the same territory the following year.

Natal Dispersal

We detected three natal dispersal events representing 2.5% recruitment of the 121 sampled nestlings. One male moved 11.6 km within the Volcanoes from its natal site to its first breeding site two years later where it was detected in 11 feathers. Its color band was read and it was a parental match to the two nestlings in the nest, confirming the first known natal dispersal in this species in North America. The bird was not detected in any samples in the interim year. A female that was sampled and color-banded as a nestling at a different nest in the Volcanoes was subsequently detected via genotyping in four feathers at its natal site two years later. The bird was a parental match to the three nestlings present. No effort was made to re-sight bands at that site, and the adult female was not detected in the interim year. The third natal dispersal event was a female that moved 254 km from its natal site in the Volcanoes to its first breeding site in the Kilbucks where it was detected based on genotyping in two molted feathers. No effort was made to re-sight color bands at that site. However, the female was a parental match to all three nestlings present and no other female genotype was detected at that site that year. The female was not detected in the interim year between fledging and breeding.

DISCUSSION

These are the first data published on Gyrfalcon nest site fidelity, breeding dispersal, and natal dispersal with known individuals in North America or in any continental Gyrfalcon population. Gyrfalcons at our study sites were highly faithful to study areas and territories but regularly moved short distances among alternate nest sites. Three instances

of natal dispersal demonstrated that Gyrfalcons undertook both long distance and short-distance movements from their natal areas to their first breeding site. Within the five-year study period, we saw a bimodal distribution of territory tenure, possibly suggesting most birds have either short (1 year) or long ($\geq$ 4 years) tenure at territories. Based on the presence of low but significant genetic structure, it appears dispersal has been limited between the Askinuks and other study areas, whereas a lack of significant structure suggests higher levels of gene flow between the Volcanoes and Kilbucks, as was corroborated by a natal dispersal event between these study areas.

Fidelity and Population Differentiation

Gyrfalcons in our study areas were philopatric to the study area in which they were first detected breeding. We observed no breeding dispersals among study areas and found significant differentiation between the Askinuks and the other two study areas. No significant differentiation was detected between the Volcanoes and Kilbucks, and we speculate that gene flow between these areas was facilitated by natal dispersal as was documented. Though there is limited information on Gyrfalcon population differentiation elsewhere, Johnson et al. (2007) used microsatellite markers and found similar, but non-significant F_{ST} values between two breeding populations in Greenland separated by 1,300 km of land, ocean, and glacier. They also found no significant structure among samples taken from northern Canada, northwest Alaska, and Norway. Possibly, the structure we observed could be a result of what appears to be highly philopatric, non-migratory populations at lower latitudes in our study areas, whereas the breeding populations sampled in Johnson et al. (2007) were from higher latitudes where Gyrfalcons are thought to be (and in Greenland, have been documented to be) more migratory.

Gyrfalcons were assumed to be faithful to territories, but the only previously available information to support this was from two banded females in Iceland (Nielsen 1991). Data from 24 individuals in our study area over five years corroborate this assumption. All males and all but one female that we detected across all sites in

subsequent years returned to their previous breeding areas. The female that dispersed had been captured and harnessed with a transmitter two years prior to the dispersal event. However, the bird escaped from the harness and successfully bred at the same site the subsequent year before dispersing the following year. Hence, we think it is unlikely, though not impossible, that the bird's breeding movements were influenced by it being harnessed two years prior to its dispersal.

Our territory tenure data showed a bi-modal distribution that allows for a number of non-mutually exclusive interpretations. First, the bi-modal distribution could be a sampling artifact from detecting individuals at the very end or beginning of their tenure during our relatively short, five-year study. The data could also reflect a dichotomy in individual fitness, site quality, or an interaction of the two. We speculate the sampling artifact explanation is unlikely, though we will be able to assess this with future years of data. Others have documented a dichotomy in individual effort or reproductive success in raptors; often a relatively small proportion of a population is responsible for the majority of offspring (Newton 1986, Jenkins and Jackman 2006, Rosenfield et al. 2009). Birds in our study areas could be behaving similarly, with a minority of birds occupying the same territory and reproducing for many years while the majority occupy territories and breed for only one or a few years. Additional years of data on this long-lived species will be needed to assess this.

Breeding Dispersal

Although Gyrfalcons were highly faithful to territories, they frequently dispersed among alternate nest sites within a territory, a common behavior in raptors (Newton 1979). Like other North American falcons (Warkentin et al. 1991, Lehman et al. 2000), Gyrfalcons moved to alternate nests after both successful and failed breeding attempts and provided us no strong evidence to suggest movements were influenced by nest fate.

The difference in mean dispersal distance among alternate nests in the Askinuks and Volcanoes was 1130 m, though it was technically non-significant ($P = 0.08$). However, we interpreted these data to suggest that in general, Gyrfalcons in the Askinuks

dispersed further than conspecifics in the Volcanoes. This would be in concordance with differences in mean inter-nest distance, which was greater in the Askinuks than the Volcanoes (8.5 km versus 4.7 km; BJM unpub. data). We speculate this difference is a result of a lower density of cliff-nesting habitat and possibly, lower prey availability in the Askinuks. Accordingly, dispersal distances among alternate nest sites in other study areas may likewise vary according to cliff and prey availability.

Natal Dispersal

Natal dispersal is one of the most intriguing, important, and unknown aspects of life history ecology (Penteriani and Delgado 2009). Though relatively little can be inferred from documenting the first three instances of known natal dispersal in North America, these data begin to identify the spatial scale and variation present in Gyrfalcon natal dispersal and allow us some insight into this largely unknown process. For example, it is interesting to note that none of the three dispersers were detected in molted feathers until two years after they fledged and all three were present in the breeding population at the end of their second year. The only other information on Gyrfalcon natal dispersal comes from two males and two females that were re-sighted in Iceland 14 km, 25 km, 53km, and 84 km from their natal site, respectively (Nielsen 1991). The dispersals documented here are both lower and higher than those of Nielsen (1991), though little can be inferred from such small samples sizes and differences in scale because Gyrfalcons in Iceland are genetically distinct from other populations (Johnson et al. 2007) and have different dispersal behaviors than their continental conspecifics (Nielsen 1986, Cade et al. 1998). Hence, it may not be prudent to assume natal dispersal behaviors documented in Iceland are similar to those found in continental populations.

Potential Biases

Two components of detection probability may have biased our estimates. First, individuals that moved beyond our study areas were not available to be detected. This

likely biased the range of our natal dispersal estimates downward because juvenile Gyrfalcons are known to undertake long distance, sometimes inter-continental movements (McIntyre et al. 2009). Such movements would not have been detected within the geographic scope of this study. Our breeding dispersal estimates could also be biased low for the same reason, though if birds regularly dispersed long distances between breeding sites, we would have expected to detect at least a few such movements among study areas. Our recruitment estimate should be considered a minimum estimate because natal dispersals beyond our study areas could not be detected. Second, even if an individual was available to be detected in our study areas, we may have failed to detect it. This may not have affected our short-distance breeding dispersal estimates because any bird missed within our study areas was likely a random event and because we searched the entire extent of each study area. However, failing to detect an individual that was present may have inflated our estimates of fidelity because birds that dispersed to new sites were probably less likely to be detected than birds that returned to previously used sites.

Implications

Documenting the frequency and distance of breeding dispersal has important ramifications when interpreting historical survey data, inferring population status, and assessing population connectivity. For example, movements of unmarked birds among occupied territories across years, especially in topographically complex areas, can complicate or prevent delineating putative territories. If territories cannot be delineated, determining occupancy or productivity status of territories across years may not be possible. Even if boundaries are known, conclusions about population status may be incorrect if occupancy history of individuals is unknown. For example, high rates of turnover indicating high adult mortality may go unnoticed if individual identity is unknown. Further, evaluating genetic exchange among populations with known individuals or indirect assessments of genetic differentiation has important ramifications for identifying and prioritizing biodiversity (Kerr et al. 2002, Cowie and Holland 2006).

Falcons in North America demonstrate a generally increasing trend of territory fidelity with body size, and our data on the largest species corroborate this trend. The smallest continental falcons, the American Kestrel (*F. sparverius*) and Merlin (*F. columbarius*) displayed moderate levels of territory fidelity (20 - 70%) (Hodson 1976, Bowman et al. 1987, Toland and Elder 1987, James et al. 1989). Though little information is available for the intermediate sized Aplomado Falcon (*F. femoralis*), Prairie Falcons (*F. mexicanus*) displayed generally higher, though variable fidelity rates from 43 - 88% (Runde 1987, Lehman et al. 2000). Peregrine Falcons (*F. peregrinus*), the second largest falcon species in which female size overlaps that of male Gyrfalcons, are highly site faithful with 93 - 98% of adults returning to the same territory (Ambrose and Riddle 1988, Enderson and Craig 1988). Gyrfalcons in this study matched the highest known territory fidelity rate documented in North American falcons (98%, *F. p. tundrius* (Court 1986)).

Recruitment rates of nestlings into the breeding population display an opposite trend with smaller species exhibiting higher rates. Though data on recruitment are relatively sparse, estimates for Merlins and American Kestrels range from 1.5 - 10% (Bowman et al. 1987, Lieske et al. 2000), whereas those for the larger species (Prairie and Peregrine Falcons) ranged from 1.4 - 2.5% (Lehman et al. 2000, Restani and Mattox 2000). Our estimate for Gyrfalcons lends further support to this general trend. This potential relationship is consistent with differing life history strategies between r and k-selected species (MacArthur and Wilson 1967). In falcons, small species (American Kestrels and Merlin, r-selected) with short life spans and relatively high annual mortality rates display high recruitment rates because of the many vacancies in the breeding population left after the death of previous breeder (Newton 1979). Larger species (Prairie, Peregrine, and Gyrfalcon, k-selected) with longer life spans and lower annual mortality rates display lower recruitment rates similar to what we documented because there are fewer opportunities to replace breeders who have died.

Little is known about dispersal and fidelity in Gyrfalcons and other raptor species because following individuals across large spatial and temporal scales is difficult

(Morrison and Wood 2009). Gyrfalcons are particularly challenging because they breed in remote, difficult to access areas under harsh conditions at low densities (Booms et al. 2008a). Our estimates are the first published on Gyrfalcon nest site fidelity and breeding and natal dispersal with known individuals in North America or in any continental Gyrfalcon population that we are aware of. As such, the estimates are important because they are the first documentation of these fundemental life history traits in this species. Further, they provide a foundation from which to better understand breeding season survey results, population dynamics, and population demography and therefore, will be useful for surveying, monitoring, and conserving the species.

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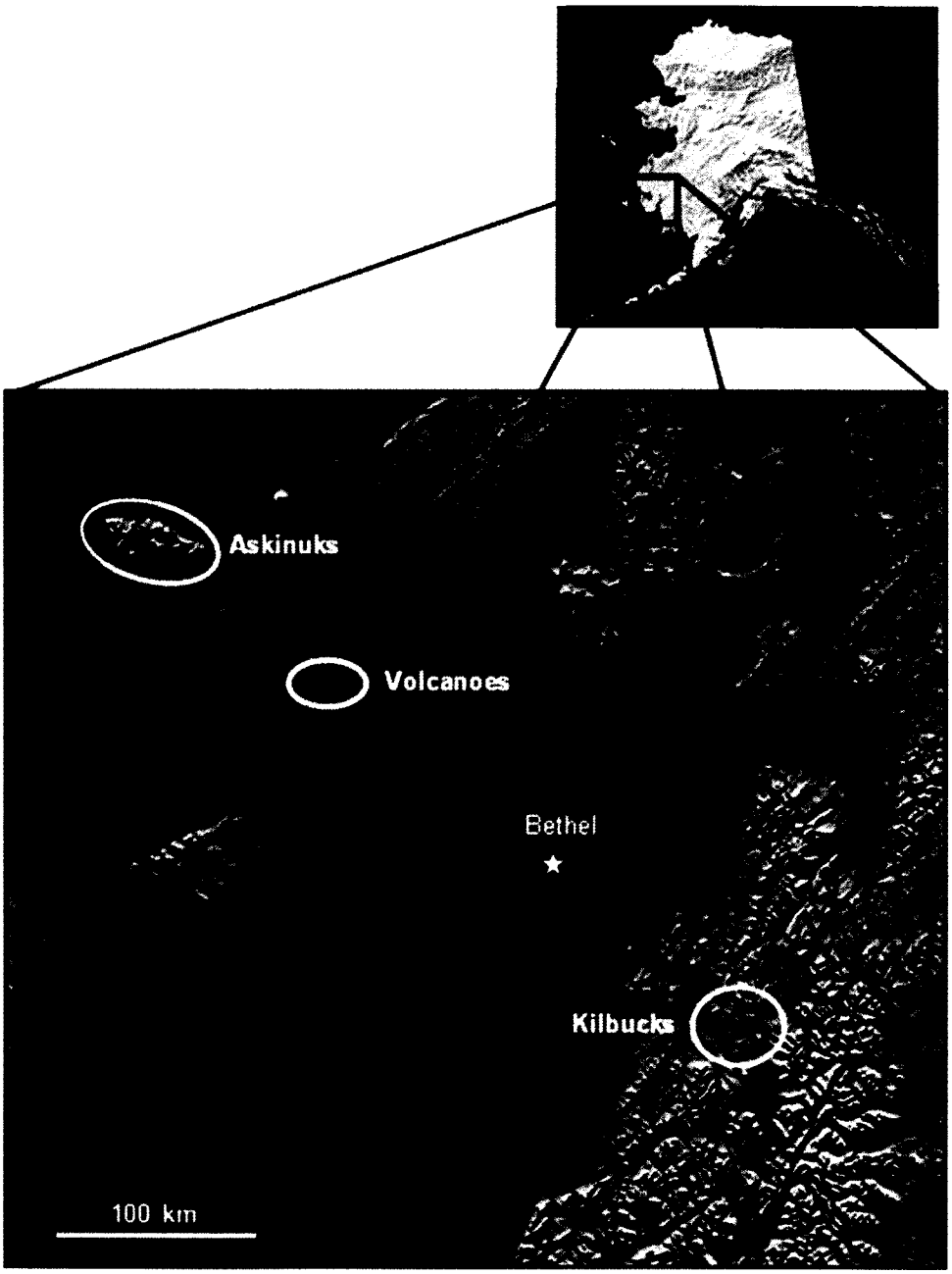

Figure 4.1. Study Areas. The location of the three study areas used to study Gyrfalcons from 2003-2007 on the Yukon Delta National Wildlife Refuge in western Alaska.

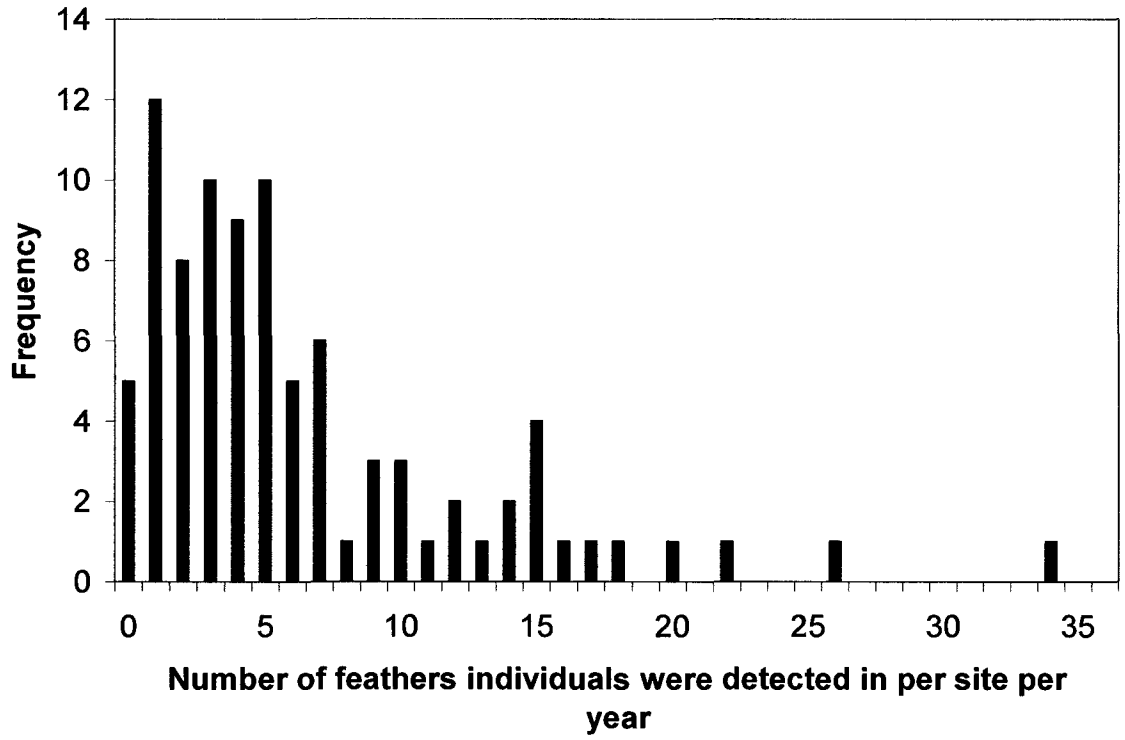

Figure 4.2. Summary of Feather Collections. Number of feathers in which unique individual Gyrfalcons were detected per territory/year on Yukon Delta NWR from 2003 - 2007. Individuals detected in zero feathers in one year were determined to be present based on one of the following: A) incomplete genotypes obtained from feathers from that area that year, B) the presence of no competing complete genotypes of other unique individuals obtained in samples in that area that year, C) were parental matches to nestlings, or D) in one case, was confirmed by re-sighting a color band.

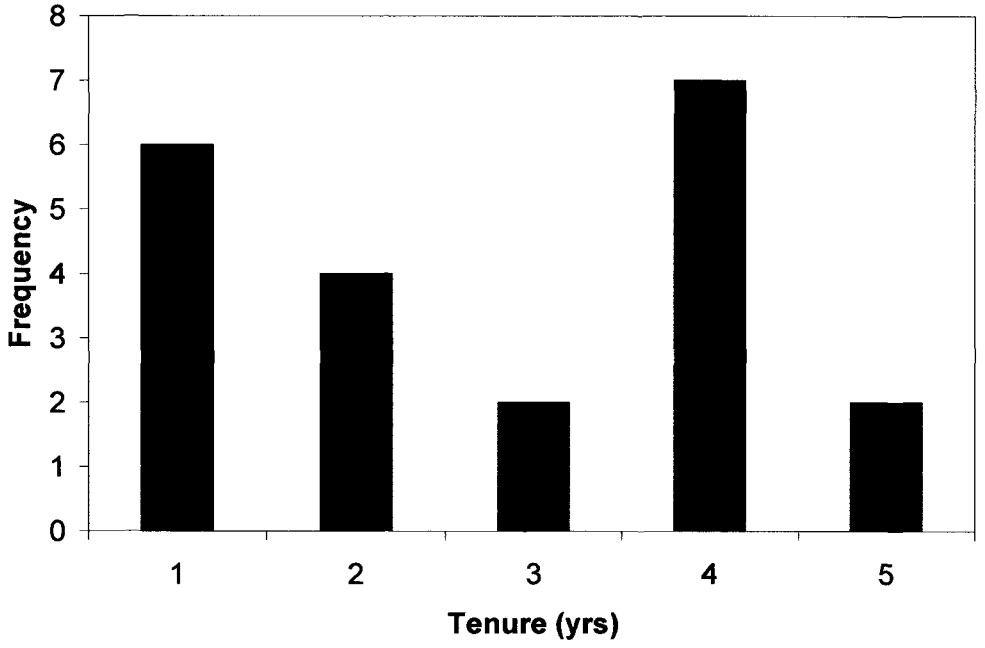

Figure 4.3. Tenure Summary. Total number of consecutive years for which a unique individual Gyrfalcon was detected at the same territory in the Volcanoes study area on the Yukon Delta NWR from 2003-2007.

Table 4.1 Samples Summary Statistics. Number of adult Gyrfalcon feathers collected per nest area per year on the Yukon Delta National Wildlife Refuge, 2003-2007.

Study Area		2003	2004	2005	2006	2007	Totals
Volcanoes							
	Number of known occupied territories	7	9	8	8	9	41
	Number of territories from which feathers were collected	6	8	8	8	9	39
	Total number of feathers collected	31	69	223	220	437	980
	Mean number of feathers collected per nest area	5	9	28	28	49	24
	Minimum and maximum number of feathers collected per nest area	0, 14	0, 19	16, 45	11, 37	17, 92	0, 92
Askinuks							
	Number of known occupied territories	-	-	-	9	8	17
	Number of territories from which feathers were obtained				9	8	17
	Total number of feathers collected				188	135	323
	Mean number of feathers collected per nest area				21	17	19
	Minimum and maximum number of feathers collected per nest area				6, 44	1, 38	1, 44
Kilbucks							
	Number of known occupied territories	-	-	7	5	-	12
	Number of territories from which feathers were obtained			7	4		11
	Total number of feathers collected			27	17		44
	Mean number of feathers collected per nest area			4	4		4
	Minimum and maximum number of feathers collected per nest area			1, 7	0, 7		0, 7

Table 4.2 Unique Individuals Summary. Summary of the number of unique individuals detected in molted Gyrfalcon feathers in the Askinuks and Volcanoe study areas, 2003-2007 and the number of occasion in which they were detected.

Unique Individuals	Number Detected in One Year	Number Detected in Multiple Years	Totals
Males	9	10	19
Occasions detected[a]	9	28	37
Females	10	14	24
Occasions detected	10	42	52
Males and Females	19	24	43
Occasions detected	19	70	89

a. An occasion is defined as the detection of a unique individual at one territory in one year

Table 4.3. Nestling Samples Summary. Number of Gyrfalcon broods and nestlings present and sampled for genetics on the Yukon Delta National Wildlife Refuge, AK 2003-2007.

Study Area	2003 Present	2003 Sampled	2004 Present	2004 Sampled	2005 Present	2005 Sampled	2006 Present	2006 Sampled	2007 Present	2007 Sampled	Total Present	Total Sampled
Askinuks												
Number of broods	-	-	-	-	-	-	6	4	6	6	12	10
Number of nestlings							14	10	17	17	31	27
Volcanoes												
Number of broods	6	0[a]	9	9	7	7	4	4	6	6	32	26
Number of nestlings	15	0	27	27	17	17	11	10	19	19	89	73
Kilbucks												
Number of broods	-	-	-	-	6	4	4	4	-	-	10	8
Number of nestlings					12	8	14	13			26	21
Totals												
Number of broods	6	0	9	9	13	11	14	12	12	12	54	44
Number of nestlings	15	0	27	27	29	25	39	33	36	36	146	121

[a] All nestlings were fledglings when surveyed, no broods or nestlings sampled in 2003.

Table 4.4 Microsatellite Markers. Summary of the microsatellite markers used to identify individual Gyrfalcons on the Yukon Delta National Wildlife Refuge, AK 2003-2007.

Locus	Range in allele size (bases)	Number of alleles	Observed Heterozygosity	Expected Heterozygosity	Probability of Identity (PID)
FP13	118-124	4	0.36	0.46	0.31
FP34	168-174	4	0.52	0.51	0.37
FP54	109-145	11	0.71	0.82	0.04
FP79-4	171-183	6	0.62	0.60	0.23
FP82-2	157-169	5	0.48	0.55	0.21
FP89-2	141-163	5	0.36	0.35	0.48
Fp92-1	129-139	4	0.19	0.19	0.7
Combined	-	-			0.91×10^{-5}

Table 4.5. Population Structure. Pairwise F_{ST} and R_{ST} values from Gyrfalcons sampled among three study areas on the Yukon Delta National Wildlife Refuge, AK, 2003-2007. Significant values following correction for multiple comparisions indicated in bold.

	Askinuks	Volcanoes	Kilbucks
Askinuks			
F_{ST}	-		
R_{ST}	-		
Volcanoes			
F_{ST}	**0.040**[a]	-	
R_{ST}	**0.209**[b]	-	
Kilbucks			
F_{ST}	**0.069**[a]	0.003	-
R_{ST}	**0.333**[b]	-0.015	-

a. $P < 0.01$
b. $P < 0.001$

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Conclusion

Science is a process and I consider this dissertation a beginning rather than an end. Long-term studies are relatively uncommon, particularly as part of a graduate degree. However, long-term studies have often provided the foundations for conservation biology, wildlife biology, ecology, evolution, and others fields of study. The degree to which long-term studies can contribute to these fields rests partially on the ease with which they can be conducted because this often determines the project's productivity. Clearly, a long-term study of Gyrfalcon breeding biology is a poor choice if one wishes to maximize scientific output. The numerous logistical challenges provided by their life history and their remote, harsh habitats, along with the lack of extensive previously published data greatly limits the amount of information that can be obtained relative to other species or systems. However, that does not diminish the need to further our understanding of this enigmatic species, particularly in the face of substantial changes that are predicted to occur in the Arctic habitats upon which it relies as global climate change advances. The chapters of this dissertation are not huge leaps of scientific discovery; they are small contributions earned through tremendous effort and dedication. In the future, I am hopeful that others and I can build upon these modest steps to advance our ability to study, understand, and conserve this and other species and, ultimately, continue the process of science.

In Chapter 1, I provided a comprehensive summary of our understanding of the Gyrfalcon in North America based on all scientific publications through 2007, many unpublished reports and datasets, and my personal knowledge of the species based on over 3,000 hours of field observation.

In Chapter 2, I created a spatially explicit model that predicted Gyrfalcon breeding distribution and population size across Alaska. The model predicted that 75% and 7% of the state had a relative index of nest occurrence of $< 20\%$ and $> 60\%$, respectively, helping to focus management efforts geographically. Areas of high

predicted occurrence primarily occurred in northern and western Alaska. The model estimated the size of the breeding Gyrfalcon population in Alaska is 546 ± 180 pairs. The model was 67% accurate with an area under the curve (AUC) score of 0.76 when assessed with real-world, independent data, which suggests the model was moderately accurate and will be useful for management decisions. This model represents the largest collection of historical raptor nest locations used for spatially explicit predictive modeling in Alaska and probably North America.

In Chapter 3, I reported results of repeated aerial surveys that estimated survey detection probability of cliff-nesting raptors from helicopters and fixed-wing aircrafts. Gyrfalcons were the most detectable species (helicopter $\hat{p}$ =0.79 (0.03), followed by Golden Eagles (helicopter $\hat{p}$ =0.68 (0.06)), Common Ravens (helicopter $\hat{p}$ =0.45 (0.10)), and Rough-legged Hawks (helicopter $\hat{p}$ =0.10 (0.14)). However, detection probability estimates for the later two species were much higher when surveyed in the second study area by fixed-wing aircraft. Detectability of all species varied by observer experience and study area/aircraft type. Fixed-wing aircraft provided reasonable detection probability estimates with relatively small SEs and should be considered for future surveys, especially in topographically simple study areas. Overall, I documented that cliff-nesting raptors are detected imperfectly, that imperfect detection can be estimated and accounted for, and that imperfect detection was influenced by a variety of other factors. I concluded that it is prudent and preferable to estimate detection probability directly in future cliff-nesting raptor surveys whenever possible if the surveys are conducted for the purpose of population monitoring.

In the final chapter, I described Gyrfalcon nest site fidelity, breeding dispersal, and natal dispersal using adult molted feathers as non-invasive genetic samples and nestling blood samples in a mark-recapture framework. I used microsatellite markers to obtain 7-locus genotypes from feathers and blood samples that provided us a mean probability of identity (unbiased P_{ID}) of 0.91 $x10^{-5}$. Genotypes were used to identify individuals across space and time in a mark-recapture context and to investigate genetic connectivity among study areas. Gyrfalcons were highly faithful to study areas and

territories; we found no breeding dispersal events among study areas and only one dispersal event between territories (98% territory fidelity). However, within territories, only 22% of birds returned to the same nest site the following year. The remaining 78% dispersed 50 - 3,400 m from the previous nest site. Dispersal distance averaged 750 ± 870m, and was similar between sexes (females 754 ± 950m, n = 19; males 745 ± 740m, n = 10). Mean territory tenure was 2.8 ± 1.4 yrs, was similar between sexes (males 2.6 ± 1.3 yrs, females 2.9 ± 1.6 yrs), and displayed a bimodal distribution with peaks at 1 and 4 yrs at the Volcanoes. Mean annual turnover rate at the Volcanoes was 20%. We detected three natal dispersal events ranging from 0-254 km representing 2.5% recruitment of the 121 sampled nestlings. Gyrfalcons in the Askinuks study area were significantly differentiated from conspecifics in the Volcanoes and Kilbucks study areas (F_{ST} =0.04 and 0.07, respectively, $P < 0.01$, $R_{ST} = 0.21$ and 0.33, respectively, $P < 0.001$), suggesting limited movement in or out of the Askinuks. We detected no significant genetic structure between Gyrfalcons in the Volcanoes and Kilbucks study areas and documented one natal dispersal event with a known individual between these study areas, confirming genetic exchange. These data are the first published on Gyrfalcon nest site fidelity and breeding and natal dispersal in North America.